Human predatory behavior and the social implications of communal hunting based on evidence from the TD10.2 bison bone bed at Gran Dolina (Atapuerca, Spain)

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A B S T R A C T
Zooarchaeological research is an important tool in reconstructing subsistence, as well as for inferring relevant aspects regarding social behavior in the past. The organization of hunting parties, forms of predation (number and rate of animals slaughtered), and the technology used (tactics and tools) must be taken into account in the identification and classification of hunting methods in prehistory. The archeological recognition of communal hunting reflects an interest in evolutionary terms and their inherent implications for anticipatory capacities, social complexity, and the development of cognitive tools, such as articulated language. Late and Middle Paleolithic faunal assemblages in Europe have produced convincing evidence of communal hunting of large ungulates allowing for the formation of hypotheses concerning the skills of Neanderthals anatomically modern humans as social predators. However, the emergence of this cooperative behavior is not currently understood. Here, faunal analysis, based on traditional/long-established zooarchaeological methods, of nearly 25,000 faunal remains from the "bison bone bed" layer of the TD10.2 sub-unit at Gran Dolina, Atapuerca (Spain) is presented. In addition, other datasets related to the archeo-stratigraphy, paleo-landscape, paleo-environmental proxies, lithic assemblage, and ethno-archaeological information of communal hunting have been considered in order to adopt a holistic approach to an investigation of the subsistence strategies developed during deposition of the archeological remains.

The results indicate a monospecific assemblage heavily dominated by axial bison elements. The abundance of anthropogenic modifications and the anatomical profile are in concordance with early primary access to carcasses and the development of systematic butchering focused on the exploitation of meat and fat for transportation of high-yield elements to somewhere out of the cave. Together with a catastrophic and seasonal mortality pattern, the results indicate the procurement of bison by communal hunting as early as circa 400 kyr. This suggests that the cognitive, social, and technological capabilities required for successful communal hunting were at least fully developed among the pre-Neanderthal paleodeme of Atapuerca during the Lower Paleolithic. Similarly, the early existence of mass communal hunting as a predation technique informs our understanding of the early emergence of predatory skills similar to those exhibited by modern communal hunters.

Resumen: La zooarqueología es una importante herramienta para la reconstrucción de la subsistencia y también para inferir aspectos relevantes del comportamiento social en el pasado. En este trabajo presentamos el análisis faunístico del llamado "lecho de huesos de bisonte", contenido en la subunidad TD10.2

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1. Introduction

There is strong evidence for hunting as the regular form of accessing animal carcasses from the early Pleistocene (Bunn, 1981, 2001; Bunn and Kroll, 1986; Domínguez-Rodrigo et al., 2005, 2007, 2009a, 2010, 2014; Domínguez-Rodrigo and Barba, 2006; Pickering et al., 2007; Sahnouni et al., 2013). It can be assumed from this that all subsequent hominins had the ability to be effective hunters. In fact, archeological evidence from recent decades has further confirmed the hunting capabilities of Middle Paleolithic/Middle Stone Age (MP/MSA) hominins (Speth and Tchernov, 2001; Bunn and Kroll, 1986; Domínguez-Rodrigo et al., 2005, 2007, 2015; Van Kolfschoten et al., 2015). By contrast, there is less information concerning hunting behavior and its social implications during the Lower Paleolithic (LP), especially within the European context, although several sites, such as Schöningen, suggest the existence of complex dynamics (Thieme, 1999; Voormolen, 2008; Conard et al., 2015; Van Kolfschoten et al., 2015).

1.1. The communal hunt

Among the many strategies for the procurement of prey, communal hunting has been proposed as part of the subsistence repertoire of Mousterian groups at the end of the European MP, especially during Marine Isotope Stage (MIS) 5 (Jaubert et al., 1990, 2005; Farizy et al., 1994; Brugal, 1995; Gaudzinski, 1995, 1996, 2005; Costamagno et al., 2006; Rendu et al., 2009, 2012; Discamps et al., 2011; White et al., 2016). This strategy has also been proposed for some assemblages of the MSA in South Africa (Klein, 1978, 1999; Klein and Cruz-Uribe, 1996; Weaver et al., 2011a).

Following Driver (1995), the social organization of hunting parties, the form of predation (number and rate of animals slaughtered), and the technology used (tactics and tools) must be taken into account to identify and classify hunting methods in prehistory. In this work, communal hunting is considered as a technique that requires the participation of several people, including those that usually do not participate in hunting parties, to kill several prey animals in a single event, often seasonally (Driver, 1990, 1995; Steele and Baker, 1993). In this sense, zooarchaeological testing of the remains resulting from this hunting practice provides valuable information concerning cognitive development, social integration, cooperation among group members, and other aspects of behavior beyond the strictly economical.

Ethnographic data indicate that communal hunting occurs for different economic, social, cultural, and symbolic reasons (Forbis, 1978; Speth, 1983, 1997, 2013; Driver, 1995). When the goal is to obtain a large quantity of meat to store (Binford, 1978; Driver, 1990) or be consumed in a place of aggregation (Prison and Todd, 1987), a communal hunt (1) exhibits large numbers of slaughtered individuals of the same species (Driver, 1995; Speth, 1997; Frison, 2004; Lubinski, 2013), (2) presents catastrophic mortality profiles, usually with a marked seasonality in deaths (Prison and Reher, 1970; Reher, 1970), and (3) displays a pattern of selective exploitation of carcasses and the systematic transportation of elements of greater nutritional value to the camps (David and Enloe, 1993; Costamagno, 1999).

The deep knowledge of environments, prey behavior, and seasonal biological cycles of the prey, necessary to perform successful communal kills, is strongly linked with anticipation capacity, social complexity, and the development of cognitive tools, such as articulated language, that are not fully recognized in Neanderthals and their relatives (Binford, 1982, 1989; Strauss, 1997; Morin, 2004). In fact, traditionally it has been thought that communal hunting was exclusively a modern human behavior that was developed during the Upper Paleolithic as part of the “human revolution” (Binford, 1982, 1985, 1989; Mellars, 1996, 2004). However, as mentioned above, European Mousterian sites associated with convincing evidence of communal hunting are common (Farizy et al., 1994; Brugal, 1995; Grayson and Delpech, 1998; Jaubert et al., 2005; Gaudzinski and Niven, 2009; Niven et al., 2012; Rendu et al., 2012; White et al., 2016), suggesting that the skills and the cognitive capacities for the development of complex hunting techniques of MP hominins were similar to those observed among other “modern” communal hunters.

Some of the technological, anatomical, and behavioral features of MP hominins emerge in transitional moments between the LP and MP (Roberts and Parfitt, 1999; Thieme, 1999; White and
Ashton, 2003; Hublin, 2009; Stiner et al., 2009, 2011; Moncel et al., 2011, 2012; Fontana et al., 2013; Stiner, 2013; Arsuaga et al., 2014). Among those that are linked with social behavior, the Middle Pleistocene hominin record of Sima de los Huesos (Atapuerca, Spain) has offered evidence of conspecífic care (Gracia et al., 2009), communicative capacities and possible symbolic behavior (Carbonell and Mosquera, 2006; Martínez et al., 2013; Sala et al., 2015) around 430 ka (Arsuaga et al., 2014). The zooarchaeological analysis of the broadly contemporary Gran Dolina TD10.2 sub-unit allows for the evaluation of the economic and social behavior of pre-Neanderthal populations of Atapuerca through the study of a faunal assemblage heavily dominated by a single species of large ungulate. The evidence allows for a discussion of the emergence of communal hunting as a paleoeconomic strategy and its implications for LP social behavior.

2. Gran Dolina TD10.2

Gran Dolina cave is one of the many karstic formations located in the Sierra de Atapuerca in the northern section of the Iberian Peninsula (Fig. 1a). The cave is of phreatic origin and more than 20 m deep with “keyhole” section morphology. Internal and external deposits fill the cavity, which was discovered in the early 20th century after being cut through during the construction of a railway. Gran Dolina has now collapsed, and upon first glance, far too little remains of the walls and roof in order to reconstruct its original geometry. According to Mallol and Carbonell (2008), “preliminary hypotheses regarding site formation are based on the dip of the sediments, the direction of debris flows, and the accumulation of great amounts of limestone rubble around what appears to have been the original mouth of the cave” (p. 13). Gran Dolina presents an oval morphology with more than 100 m² of surface excavation, but the total extent of the surface and the original morphology are presently unknown. There is evidence that the current surface could be doubled on the upper levels (Ortega, 2009). Eleven stratigraphic units have been identified, from the base to the top (TD1—TD11) (Gil et al., 1987; Pares and Pera-González, 1999; Pérez-González et al., 2001), and subsequently revised (Rodríguez et al., 2011; Campañá et al., in press; Vallverdú & Poch, in press) (Fig. 1b). The 3 m thick lithostratigraphic unit TD10 is the youngest archeo-paleontological level and is divided into four lithostratigraphic sub-units named from top to bottom (TD10.1—TD10.4). Geo-chronological studies suggest that the sequence falls into MIS 11—9 (Falguères et al., 2001; Berger et al.,

![Figure 1. Location and stratigraphic section of Gran Dolina (Atapuerca): a) map of the location of Gran Dolina in the north of the Iberian Peninsula, b) stratigraphic schematic view of the cave's paleo-morphology from the railway trench (archaeological south) section, c) synthetic stratigraphic profile with the locations of the available ESR-U/Th, TL-IRSL and ESR-OB dates from Falguères et al. (1999), Berger et al. (2008) and Moreno et al. (2015). Legend: (1) Mesozoic limestone on the roof of Gran Dolina; (2) speleothem; (3) lutites, clay loam/terra rossa; (4) bat guano; (5) laminated loamy clays; (6) calcilutites and calcarenites; (7) gravel and boulders, clastic flow; (8) arrangement of fallen boulders; (9) main stratigraphic discontinuity; (10) secondary unconformity and loamy-clayey-sandy filling; (11) Matsuyma-Brunhes boundary; (12) disappearance of Mimomys savini and first occurrence of Iberomys brecicensis; (13) location of the samples for dating; in brown the lithostratigraphic unit of TD10; in pink the lithostratigraphic sub-unit TD10.2 (modified from Berger et al., op. cit.: 302).]
2008; Moreno et al., 2015)(Fig. 1c). By the summer of 2015, the sub-units TD10.1, and TD10.2 were fully excavated (~95 m²). The archeo-stratigraphic studies have shown the presence of at least eight archeo-layers in the lithostratigraphic sub-unit TD10.1 (Obregón, 2012). During fieldwork and in subsequent analyses, several archeological layers were also identified in sub-unit TD10.2. This work focuses on the most important of them in quantitative terms, referred to as the TD10.2 bone bed where more than 40,000 faunal and nearly 8000 lithic remains have been recovered. The archeological investigations of the TD10 unit until now have been focused mainly on the TD10.1 sub-unit. These studies converge on two key arguments: 1) a recurrent anthropic use of the cave as a reference place, and 2) a high variability in the nature of occupations, from ephemeral and low intensity to prolonged and intense (Rosell, 2001; Menéndez, 2010; Blasco, 2011; López-Ortega et al., 2011; Obregón, 2012; Olle et al., 2013; Terradillos-Bernal, 2013; Rodríguez-Hidalgo, 2015; Rodríguez-Hidalgo et al., 2015).

Certain characters of the technological transition from Mode 2 to Mode 3 have been recognized along the sedimentary succession of TD10. These include a progressive curation of the prepared core flake production and a decreasing number of large tools resulting in a higher incidence of small flake tools, which progressively increase in standardization and morphological diversity (Menéndez, 2010; Terradillos-Bernal and Diez, 2012; Olle et al., 2013; García-Medrano et al., 2015). The significance of these evolutionary trends and their identification with an early Middle Paleolithic technology have been, however, difficult to assess up to now (Olle et al., 2016).

What is clear is that while throughout TD10, the lithic assemblages seem to share a similar pattern for procurement strategies defined by the decisive selection and management of raw materials, TD10.2 shows evidence of strikingly marked specialization: chert is overwhelmingly dominant over other raw materials, accounting for 98% of the assemblage. Quartzite and sandstone usually appear in very low percentages (and, interestingly, sometimes in the form of large, shaped tools). All of the raw materials have local origins in a radius less than 2.5 km (García-Antón, 2016), although the potential primary source of the chert is closest to the cave, barely 350 m away. In TD10.2, complete production sequences have been documented for chert, with relatively scarce cores, a large proportion of flaking products and waste, and a moderate quantity of frequently retouched flakes. Centripetal reduction is predominant over other methods and is found mainly through bifacial strategies, occasionally showing a certain hierarchy of flaking faces. Denticulates, side-scrapers, and points are the most represented flake tools, among which a standardized group of denticulate and carinated points stands out (Olle et al., 2013). The regular use of bone as simple percussion tools in the form of bone retouchers has been documented (Rodríguez-Hidalgo et al., 2013a).

Sub-unit TD10.2, the focus of this research, consists of a red-mud matrix with limestone boulders about 1 m thick. The layer immediately above the bone bed studied here has two electron spin resonance/uranium-series (ESR/U-series) dates (418 ± 63 ka and 337 ± 51 ka) (Falguères et al., 1999). Two recent ESR dates on quartz grains have been obtained for the same layer and for the bone bed itself (375 ± 37 ka and 378 ± 10 ka, respectively) (Moreno et al., 2015). However, optically stimulated luminescence (OSL) has provided a slightly discordant mean date of 244 ± 26 ka for this layer (Berger et al., 2008) (Fig. 1c). Ongoing combined single-grain TT-OSL and pIR-IR studies (Arnold et al., 2015) comprising the whole TD10 succession will hopefully shed light on these discordances.

3. Materials and methods

During the excavation of the Gran Dolina TD10.2 sub-unit, all faunal remains longer than 2 cm and all identifiable remains (e.g., individual teeth) have been recovered and coordinated in three-dimensional space using a 3-Coor system (Canals, 2008). The excavation protocol at Gran Dolina does not typically piece-plot mesovertebrates (e.g., leporids and small birds). These remains were placed in bone collection bags each day, recording square and depth, together with non-identifiable macromammal remains less than 2 cm. The contents of these bone collections are not included in this paper, but have been analyzed and reported by Rodríguez-Hidalgo (2015). Nevertheless, although several specialists assisted the excavation team with faunal determinations during the course of the fieldwork, mesovertebrate remains (mainly complete bones of rabbits) were occasionally recovered in situ and piece-plotted by error. These remains have been included here to test the role of small taxa in the accumulation and provide preliminary results; specific research concerning the mesovertebrates is in preparation.

An archeo-stratigraphic approach was used for the faunal remains in the TD10.2 sub-unit to re-define the archeological levels that were observed during fieldwork based on a method developed by other colleagues (Canals, 1993; Canals and Galobart, 2003; Obregon and Canals, 2007). ArchePlotter is a 3.5.4-beta software developed by Catalan Institute of Human Paleoeconomy and Social Evolution (IPHES for its acronym in Catalan) was used to plot profile data. The three-dimensional coordinates of the faunal remains and other objects (e.g., lithic artefacts, limestone boulders) were plotted along two-dimensional projection planes. ArchePlotter enabled oblique vertical projections in relation to the excavation plane. The faunal record of the TD10.2 sub-unit is composed of more than 65,000 coordinate specimens of which more than 40,000 belong to a single archeological level, circa 20 cm thick and named by the fieldwork team the “bison bone bed” (blue crosses in Fig. 2). Sparse archeo-stratigraphic definition of this archeo-layer on the periphery of the excavation area (archeological squares of 1 m × 1 m in the W and SW extremes of the excavation area, Figure 2 projection I–I’ and S in lateral projection III–III’) has been documented so that materials in the periphery can be disregarded in this work, because it cannot be guaranteed that all materials in the periphery of the main accumulation belong to the bone bed layer. Similarly, some faunal remains from squares 15–16 at the top of the bone bed have not been included in this work although, as can be seen in Figure 2 (projection II–II’), they are compatible with the bone bed remains. Therefore, the present study addresses those faunal remains (c. 25,000) that can, as of now, be placed confidently within the TD10.2 bone bed archeological layer (~70% excavated surface).

The data collected for each faunal remain were anatomical element, taxa, size, position, age, portion, and side. Five measures of abundance were used: Number of Specimens (NSP), which includes the total number of faunal remains independently of their identification grade (Grayson, 1984), Number of Identified Specimens (NISP), Minimal Number of Elements (MNE), Minimal Animal Units (MAU), standardized %MNE, and Minimal Number of Individuals (MNI) (Binford, 1984; Lyman, 1994).

The Shannon evenness index was calculated to explore taxonomic diversity in the assemblage. Shannon evenness is defined as (E) = −(Σ pi ln(pi))/lnS, where S is the number of species and pi is the standardized proportion of specimens of the ith species. Simpson’s Index was also determined: (D) = Σni(ni − 1)/N(N − 1), where ni is the number of specimens in the ith species and N = the total number of specimens (Magurran, 1988; Grayson and Delpech, 1998, 2002).

Non-identified specimens have been included in bone categories (long bone, flat bone, or articulated bone) and in size categories (Saladie et al., 2011). In the case of flat bones, those that showed structural features of ribs or vertebral apophyses were classified as “IFVR” (Indeterminate Flat Bones Vertebrae/Rib). To calculate MNE, the overlapping of anatomical landmarks, ontogenetic age,
Figure 2. Vertical distribution of archeo-paleontological remains from the excavated unit, TD10, at Gran Dolina. Lines I–I’, II–II’ (longitudinal), and III–III’ (lateral) represent vertical projections of 25 cm. Gray crosses indicate 3D plotted items corresponding to the TD10.1 sub-unit that were not dealt with in this work. Items from the TD10.2 sub-unit (and all remains in projection III–III’) are indicated in different colors (see legend). The dotted red line indicates the archeo-stratigraphic gap between sub-units TD10.1 and TD10.2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
side, or other features that can help to estimate the minimum number of elements in the assemblage were taken into account. In the case of long limb bones, the recommendations of Mearan and Spencer (1991), modified by Saladié et al. (2011: Fig. 1), were followed. The MNE for ribs was estimated in the same way. However, due to their characteristic anatomical configuration, it was decided to divide them into the most recognizable portions from a structural point of view. Portion 1 refers to the epiphysis (including the head, neck, and costal tubercle as landmarks), portion 2 refers to the costal angle (including intercostal muscle tuberosity and medullary cavity as landmarks), portion 3 to the proximal shaft (retaining four well-identifiable sides and no medullary cavity), portion 4 to the medial shaft (two main sides and no medullary cavity), and portion 5 to the sternal end, preserving its sides views designation (cranial, caudal, medial, and lateral).

To calculate MNI, complete dental series and isolated teeth were considered, taking into account their grade of eruption and wear (Smuts et al., 1978; Levine, 1982; Mariezkurrena, 1983; Wegrzyn and Serwatka, 1984; Hillson, 1986). Skeletal development patterns, epiphyseal fusion, and ossification following Barone (1976) have been considered.

Following Stiner (1990), the individuals have been clustered into three age groups: young, prime-adults, and old individuals. For bison, the considerations of Driver and Maxwell (2013) concerning the young age category, which is defined as animals less than two years old, have been taken into account. In this work, both fine resolution histograms for age classes divided into dental age groups (DAGs) (Frison and Reher, 1970; Reher, 1970; Klein, 1982) and "modified triangular graphs," which plot the proportional representation of three age classes with a 95% confidence interval (Steele and Weaver, 2002), have been used to represent the mortality profiles.

Based on actualism, methods for estimating the season of bison mortality assume that extinct bison were similar to modern relatives in their reproductive cycles (Reher and Frison, 1980; Wilson, 1980; Hill, 2008). The bison and wisent (Bison bison and Bison bonasus), along with other ungulates, show a pattern of births restricted seasonally and a schedule of tooth eruption, replacement, and wear well known through reference collections of extant species (Rutberg, 1984; Wegrzyn and Serwatka, 1984; Lott, 2003; Krasinska and Krasinski, 2007). Using the peak time of birth to set the calendar to zero, the dental pattern observed archeologically provides information concerning the presence of seasonal mortality in an assemblage. In turn, the gregarious behavior of bison and the special configuration of herds consisting mostly of females and their offspring (yearling and calf) for the majority of the year, favors the recognition of mass mortality events by age and sex composition in archeological/paleontological assemblages (Wilson et al., 1982; Speth, 1983; Frison and Todd, 1987; Todd, 1987).

The bison data of Kreutzer (1992) following the criteria of Morlan (1994) was used to calculate the relationship between MAU and the mineral density of portion-specific values of bones (regression and Spearman's rank-order correlations). The data concerning bison published by Emerson were used to explore the correlation between MAU and economic utility of carcass (Emerson, 1990, 1993). To facilitate comparison between assemblages, the standardized food utility index (S)FUI data from Metcalfe and Jones (1988), which includes the values for complete elements, were added to the unsaturated marrow index (UMI) from Morin (2007) to explore hypotheses related to hominin decisions about marrow procurement. Because the correlations between economic utility and skeletal part representation involve small sample sizes and usually produce type II errors (in which no correlation is found in an assemblage despite the presence of a correlation in the population assemblage), these correlations were calculated using the bootstrap regression/correlation method for some explorations. The resulting scatter plot was then interpreted in the general middle-range theoretical context of Binford's (1978) ethnoarchaeologically derived skeletal part abundance curves (Hill, 2008).

Following the protocol established by Faith and Gordon (2007), the Shannon index was calculated for "high-survival" elements. These authors argue that this uniformity index can be used as a quantitative method to discriminate assemblages characterized by subtle variations in skeletal abundance. These variations in representation could be related to butchering and transport decisions made by hominins. The repetition of the same decisions generates assemblages in which the representation of elements is related to its utility of these anatomical elements (Binford, 1978).

Following Villa and Mahieu (1991), shaft circumference, shaft length, and the fracture outline, angle, and edge were recorded to explore the nature of fragmentation observed in the assemblage. For flat bones, the same criteria were observed when enough cortical tissue and medullary cavity made this possible, as in the case of scapular neck or costal angle in the ribs (Hill, 2008). Forced surface modifications were used to assess the significance of different actors in the archeological assemblage. In the TD10.2 bone bed collection, the complete surfaces of all faunal remains were inspected macroscopically and microscopically (OPTHEC 120 Hz model, using magnifications from 15 to 45) according to recommendations provided by Blumenschine et al. (1996). For detailed bone surface observation, an ESEM Fei Quanta 600 was used (low vacuum mode using both secondary and back-scattered electron detectors). The distribution and incidence of modifications were recorded. Hominin- and carnivore-induced damage was noted in terms of the anatomical area and the region (portion and side) of the modifications. Cut marks were identified based on the criteria of Binford (1981), Potts and Shipman (1981), Shipman and Rose (1983), and Domínguez-Rodrigo et al. (2009b). In the TD10.2 assemblage, four types of cut marks were detected: incisions, sawing marks, scraping marks, and chop-marks. The type, delineation, situation, and position of the cut marks on the skeleton allow for the identification of several butchering activities. For this purpose, ethnoarchaeological sources (Binford, 1978, 1981; Abe, 2005), experimental data (Frison, 1974; Nilssen, 2000), butchering experiments with bison (B. bonasus) carcasses (personal observation), and analogies established with the archeological record have been used in this study (Wheat, 1972, 1978; Frison, 1974).

Surface modifications during anthropic breakage of bones were also analyzed and recorded in terms of presence/absence. These were: percussion pits (Blumenschine and Selvaggio, 1994), conchoidal scars and flakes, adhered flakes (Capaldo and Blumenschine, 1994), and peeling (White, 1992; Pickering et al., 2013). Rectangular percussion marks, which were probably formed with the edge of a dihedral tool (Domínguez-Rodrigo and Barba, 2006), and strie fields (Pickering and Egeland, 2006) were also documented. Descriptions include the location of damage on remains. Conchoidal scars and flakes were assumed to be anthropogenic when associated with percussion pits.

Hominin tooth marks were identified based on the criteria of Saladié et al. (2013a) and took into account the descriptions from Fernández-Jalvo and Andrews (2011) and Pickering et al. (2013). Human tooth marks were determined based on their morphological features, their location on the bone, and the concurrence of modifications on single bones (e.g., tooth marks associated with peeling) (Pickering et al., 2013; Saladié et al., 2013a). The presence or absence of the tooth marks on each specimen was noted. The
presence of flaking and micro-striations was described in the scores, as was the morphology of the pits and punctures (crescent, circular, or angular) (Saladié et al., 2013a).

Non-human carnivore tooth marks (hereafter carnivore tooth marks) were also present in the TD10.2 assemblage. The morphological traits of the punctures (deep, multicuspid, with a bowl-shaped transversal section) and the scores (deep, with the bottom and walls creating an irregular path), and pits (with an oval or angular morphology) (Bunn, 1981; Shipman, 1981; Blumenschine, 1995; Fisher, 1995; Domínguez-Rodrigo and Barba, 2006), along with the presence of other severe modifications on bones of bison and bison-sized animals helped in the determination of carnivorous activity in the assemblage. The presence of licking, pitting, scoring, furrowing, and scooping-out was noted (Haynes, 1980, 1983; Binford, 1981). Digested bones were also included in this group following the diagnosis and grades of Lloberas et al. (2008). Measurements of the pits, punctures, and scores were determined using the criteria of Domínguez-Rodrigo and Piqueras (2003) and Andrés et al. (2012) and compared with experimental data from Selvaggio (1994a), Delaney-Rivera et al. (2009), Andrés et al. (2012), and Saladié et al. (2013a, b).

The location, segment, portion, and side of all the anthropogenic and carnivore modifications on the bones were noted (Blumenschine and Selvaggio, 1994; Blumenschine, 1995; Domínguez-Rodrigo, 1997, 1999). Spatial Analyst ArcGIS Module tools of ArcGIS software were used to illustrate the distribution of cut marks and carnivore tooth marks on long limb bones. Following Parkinson (2013), Parkinson et al. (2014), the density tool (Kernel Density) was used to identify clusters of modifications along elements. For illustrating the distribution of modifications, Maren’s “Bone Sorter” extension for ArcView (Marean et al., 2001; Abe et al., 2002) was employed.

Because the assemblage exhibits anthropogenic marks and damage generated by carnivores, the coincidence of modification attributed to each on the bones (Egeland, 2007) and the overlapping of modifications have been taken into account to establish the degree of interdependence between agents in the formation of the assemblage. Furthermore, considering the existence of a rich carnivore guild during the European Middle Pleistocene (Turner, 1992; Croitor and Brugal, 2010), the persistence of carcasses in boreal ecosystems, the importance of carrion in certain food chains (Selva, 2004; Selva et al., 2005), and the critical role of interspecific competition that may have been present (Binford, 1981; Blumenschine et al., 1994; Domínguez-Rodrigo, 1994, 1999, 2001; Faith and Behrensmeyer, 2006; Gidna et al., 2014), a number of taphonomic indices have been implemented that allow for an estimation of the degree of carnivore ravaging of the assemblage. The ratio of shaft fragment specimens (NISP) of the limb bones in relation to specimens of the epiphysis (Marean and Spencer, 1991; Blumenschine and Marean, 1993), the percentage of change using the MNE according to Domínguez-Rodrigo et al. (2002), the ratio of axial (ribs and vertebrae) elements to the long limb bones (MNE), and the ratio of proximal humerus and distal radius to the distal humerus and proximal radius (MNE) (Domínguez-Rodrigo and Organista, 2007) have been considered.

4. Results

In this work, 24,216 faunal remains (NSP) belonging to a wide variety of taxa, including ungulates, carnivores, large rodents, leporids, birds, and reptiles have been analyzed. Despite this taxonomic diversity, as the name of the bone bed indicates, the assemblage is dominated by bison remains (22,532 or 98.4% NISP) (Table 1). More importantly, in understanding the taxonomic features of the assemblage, the other 17 taxa are represented by less than 60 specimens, each below 0.3% NISP. Only 0.1% of the remains are compatible with small and very small-sized adult animals, and the remaining 5.4% are completely indeterminable (taxonomically and anatomically).

The indices used to measure the taxonomic diversity indicate that this is an extremely uneven assemblage (E = 0.024), with a single dominant taxon (D = 0.009). Thus, the TD10.2 bison bone bed can be considered monospecific since 99% of the NISP for ungulates represents a single species. Taking into account this feature and the differences detected in the taphonomic history regarding the anthropogenic modifications (see below), henceforth, the bison data and the other specimens are presented as separate subsets, the bison-set and the non-bison remains.

In general terms, the assemblage is highly fragmented but well preserved. The conservatism of the cortical surfaces of the bones is excellent. Few post-depositional modifications have been observed with the exception of dispersed black manganese oxide/hydroxide stains, which are relatively abundant in the assemblage (70.4% NSP). These black stains may be related to the post-depositional conditions and the micro-environment of the cave, which is characterized by high humidity and soil humification by decomposing organic materials (e.g., Marín Arroyo et al., 2008), but the stains do not mechanically modify the bone surfaces or interfere with taphonomic analysis. In the interest of building taphonomic pathways, it is noted that 248 remains are rounded by hydraulic abrasion (1% NSP). These items were concentrated in an area with a small channel of low-energy water surface circulation (J. Vallverdú, personal communication). Other modifications related to bone destruction, such as dissolution (0.19%) and root etching (0.12%), or alteration of the bone surfaces, such as weathering (1.33%) and trampling (0.37%), are scarce and associated with the karstic depositional environment.

4.1. Bison-set of TD10.2

Ongoing research of the taxonomy of TD10.2 bison suggests that they represent a small form close to *Bison priscus* and are assigned presently to *Bison* sp. (J. van der Made, personal communication). The bison-set assemblage is composed of 22,532 specimens representing at least 60 individuals (figure determined from the mandibular molars). Of these, 21 were young, 36 were prime-adults, and three were old. A total of 47 complete mandibles, mandibular fragments with at least one mandibular molar, and isolated mandibular molars have been assigned to seven DAGs. Figure 3 shows the structure of the population of the TD10.2 bison-set, which is very close to a hypothetical living population estimated on the basis of observations by Prison and Reher (1976) and statistically overlaps catastrophic mortality profiles from several anthropogenic bison kills (Stiner, 1991; Driver and Maxwell, 2013). Unfortunately, the scarcity of long bone epiphyses does not permit the formation of inferences concerning the sex composition of the bison bone bed.

The estimation of seasonal mortality indicates a bimodal pattern in which most deaths are concentrated around two seasonal peaks that coincide with late spring/early summer (35% of the identified individuals) and early fall (32% of identified individuals). Regarding the micro-wear results (numbers of scratches observed and compared using Levene’s test), the assemblage from TD10.2 was found to differ significantly from the reference sample obtained from level G of Arago Cave, which represents a palimpsest of occupations occurring through a year. The TD10-2 assemblage is also significantly different from the Taubach short-term occupation;
however, there is no significant difference from the reference seasonal occupations determined for level F of Payre (reference data from Rivals et al., 2009). Consequently, the duration of accumulation of the TD10.2 bison assemblage was seasonal. Micro-wear studies also suggest a very low mortality incidence outside these two seasonal peaks. The combination of tooth eruption, wear, and micro-wear suggests an abandonment of the site between the seasonal occupations, especially during the winter (Rodríguez-Hidalgo et al., 2016).

The anatomical profile of the bison-set is characterized by the common occurrence of the axial skeleton, particularly skulls and ribs. Ribs are abundant (3892; 41% NISP), followed by isolated teeth and tooth fragments (1699; 17.9% NISP), vertebrae (1380; 14.5% NISP), skull fragments (732; 7.7% NISP), and mandibles (673; 7.1% NISP). All other skeletal elements are represented by very low values, ranging from 1.3% to 0.1% of the NISP (125 NISP or less). Especially striking is the shortage of long bones. Remains that have not been assigned to a specific anatomical element account for 13,029 specimens. These include fragments of indeterminate flat bones (IFB + IFBVR + IFBCMSI) (8207; 36.7% NISP), among which fragments of ribs and vertebral apophyses are noticeable (IFBVR (5739)). Considering all of the specimens belonging to the axial skeleton, particularly skulls and limbs in the bison-set.

An estimate of 1197 elements (MNE) has been calculated, the most numerous of which belong to low-survival elements defined by a lack of non-cancellable thick cortical portions, whose representation is associated primarily with post-depositional destruction. These include ribs (MNE = 402) and vertebrae (MNE = 272) (Table 2). Long bones are very scarce in terms of MNE (maximum MNE is 21). This is particularly true for upper limb remains (HM = 18 MNE; FM = 11 MNE). The high representation items that are rare in many other Pleistocene assemblages, such as the hyoid that is prone to disappear as a result of destructive processes, is particularly remarkable. Although an in-depth investigation of this phenomenon has not been performed, initial results indicate a random spatial distribution of anatomical elements discarded in an artificial and biased sample.

The relative abundance of bison elements (%MAU) can be graphically observed in Figure 4. Due to the fact that MAUs were calculated by standardizing the MNE values according to the number of times the part occurs in the skeleton, the over-representation of ribs is attenuated. However, the only anatomical elements that exceed 20% of the MAU belong to the axial skeleton, including the cranial segment and ribs. The %MAU of limb bones suggests a marked deficiency, especially a loss of the distal bones, such as metapodials and phalanges. The scarcity of the epiphyses of long bones, especially the least dense epiphyseal portions, such as the proximal humerus, distal radius, distal femur, and proximal tibia, suggests that mineral density-mediated attrition processes occurred during the formation of the assemblage. In contrast, the high representation of the hyoid suggests that the cranial remains are not over-represented relative to low-density elements due to attritional processes associated with mineral density, as the hyoid is an element that rarely survives such processes (Kreutzer, 1992). Despite this, and due to significant bias in anatomical representation, the assemblage has been tested for possible differential attritional processes associated with mineral density-mediated attrition processes occurring during the formation of the assemblage.
Explanation for the anatomical representation recorded at the site (Table 3).

Taking into account the scarcity of post-depositional taphonomic modification observed in the assemblage and the common presence of low survival elements in the bison-set, the anthropogenic transport decisions and the ravaging of carnivores should be considered as the main factors to explain the bias of the anatomical profile. For carnivores, destruction and subsequent ravaging is largely related to the mineral density of the elements and their portions (Grayson, 1989; Marean et al., 1992), while for hominins the expectation is to remove complete elements as units (for example, the complete femur) (Emerson, 1993).

The inspection of the relationship between the anatomical profile and the economic utility of elements in order to assess economic transport strategies is ambiguous. Although the results are not statistically significant in the majority of cases (Table 4), the linear correlation between the %MAU and (S)FUI is similar to the reverse bulk utility curve (Binford, 1978, 1988; Metcalfe and Jones, 1988; Marean, 1997; Faith and Gordon, 2007) (Fig. 5), in which high-utility elements have been transported away from the site and low-utility elements have been abandoned. In fact, an error Type II is suggested for the correlation between %MAU and economic utility due to the fact that in a bootstrap regression/correlation, the p values are much lower than 0, indicating statistically significant results with strong correlations (Table 4).

Using indicators that reduce the effects of biotic or physical post-depositional depletion of cancellous bones, long bones are unevenly represented. The evenness index (0.799) indicates low anatomical diversity in the bison-set supporting the interpretation that carcasses were selectively transported, either because transport was across a longer distance, the carcasses were acquired a

Figure 3. Mortality pattern of the bison in the TD10.2 assemblage. In the modified ternary plot (top), the overlap of the 95% confidence ellipsis of the TD10.2 bison mortality pattern with data from other bison dominated sites can be seen (from Driver and Maxell, 2013) and all are included in the catastrophic mortality area. The bar chart graphic (bottom) shows the structure of the population in terms of the dental age groups (DAGs) of the bison from TD10.2 bone bed, compared with, and closely resembling, a living population structure (after Frison and Reher, 1970).
long distance away from the “final deposition site,” because several carcasses were transported at the same time, thereby increasing the amount of transported weight. Given that the sample size is large (MNE = 200), this value is compatible with an unbiased strategy in which skeletal elements are transported in direct proportion to their economic utility.

The bison remains are very fragmented, with 94% of them less than 10 cm in length. Apart from isolated teeth, which are usually well preserved, complete items are small and compact bones, such as carpals, tarsals, phalanges, and sesamoids (NISP = 217). Fragmentation analysis was applied to a total of 2098 long bones. The results show that 84% of them are less than a quarter of the length of the shaft and less than one third of its section. In the set, there are no diaphyseal cylinders (long bones that retain more than a quarter of the original length of the shaft and the entire section). Among the total of 3647 planes of fracture, curved (57%) and longitudinal (31%) are most common, and angles of fractures are mostly oblique (51%). Smooth surfaces predominate (84%) coinciding with a green fracture of most long bones.

Given that the TD10.2 bison-set is composed of a large quantity of axial post-cranial remains, it is important to assess their fragmentation. However, the absence of specific methods for assessing the agent of fracture for this type of bone, except for those broken by peeling (White, 1992; Pickering et al., 2013), makes it difficult to provide quantitative results. However, the relationship between the NISP and MNE (Klein and Cruz-Uribe, 1984) of rib bones provides an indication of the high fragmentation of this element (3892 vs. 402). Complete ribs of adult bison (B. bonasus) are between 350 mm (Rib1) and 700 mm (Rib10). In the bison-set, only eight ribs are preserved intact, and the average length of the archeological fragments is 71 mm. A number of the fractures present in ribs are considered to be green (n = 523), although most of the rib fractures and those on flat bones appear to be due to post-depositional processes (including abundant fractures due to excavation process, n = 898).

4.1.1. Human-induced modifications In the bison-set, 1019 remains with cut marks, 390 remains with anthropogenic bone breakage (295 showing percussion marks), and 192 remains showing human tooth marks have been located (Table 5). Cut marks are present on 4.5% of the bison specimens. With the incidence of cut marks and remains (1019 cut marked specimens and more than 3200 individual signs), the TD10.2 bison bone bed presents the Lower Paleolithic assemblage with the highest number of cut marks and cut-marked specimens documented thus far. The descriptions of the location and features of the cut marks are presented in Tables 6 and 7. Morphologically, most cuts are slicing marks (n = 3050 or 90% of total cut marks), but scrape marks (n = 118), chop marks (n = 65), and saw marks (n = 3) have been observed (Fig. 6). Cut marks are present on most of the elements and are absent only on underrepresented bones and those of low utility, like carpals, tarsals, and distal phalanges. Regarding cut-marked bones, most of the cut marks are documented on rib fragments (35.7%), Indeterminate long bone fragments (17.3%) and indeterminate flat bones fragments (15.2%) were not taken into account in the anatomical representation via NISP. However, if cut-marked specimens are considered in terms of the NISP of each element, intermediate appendicular (38.7%) and proximal appendicular bones (28.6%) show the highest frequencies (Fig. 7). If the portions of the bone that are marked are taken into account, it can be observed that 76% of the cut marks are on the shafts, 18% are on portions near the epiphysis, and only 4% of cases are on the epiphyses. These frequencies and their distributions have been related to early access to fleshed carcasses (Domínguez-Rodrigo et al., 2014). The location of cut marks on limb bones can be seen in Figure 8. Kernel density analysis of cut marks on the long bones indicates that the main distribution is on “hot zones”, which suggests an intensive defleshing of these meaty portions (Binford, 1981; Potts and Shipman, 1981; Bunn and Kroll, 1986; Domínguez-Rodrigo, 1999;
Domínguez-Rodrigo and Barba, 2006; Barba and Domínguez-Rodrigo, 2008)( Fig. 9). The extension of the exploitation of the meat to elements of high-processing cost, such as the ribs and vertebrae (Marean and Cleghorn, 2003), were also observed. The intensive exploitation of large muscle packages was documented through the marks on the neural processes of the thoracic vertebrae and lateral processes of lumbar vertebrae. In the case of thoracic vertebrae, 11.4% of the neural process fragments show slicing marks related to the exploitation of the abundant meat and fat located in the hump of the bison (Lott, 2003; Krasiński and Krasińska, 2007). Cut marks on ribs were made mainly during defleshing (66%), inferred from the abundant slicing marks located in muscular insertions and along the angle and body (especially along the lateral surface). The cut marks on the cranial and caudal borders of the ribs are abundant and related to the extraction of the intercostal muscles indicating intensive exploitation. In this sense, it must be noted that although these are elements of high processing cost, they also have a high value of energy return (Emerson, 1990, 1993).

In the bison-set from the TD10.2 bone bed, other activities performed during butchering have been identified. Due to the abundance of axial elements, butchering tasks have been documented that are usually scarce in Pleistocene assemblages. In this regard, the presence of a large number of slicing marks on the lingual surface of the mandibles (20%) and on the hyoids (5%) suggests a recurrent exploitation of the tongue. As regards the trunk, 28.7% of the cut marks are located on the medial side of the rib. This pattern is associated with evisceration (Binford, 1981; Nilssen, 2000).

Other butchering tasks, such as disarticulation and dismemberment, can be inferred from the set. For example, this can be seen in the long and deep cuts in the area surrounding the acetabulum, on the iliopubic eminence, and on the pectineus surface of an os coxa of an adult bison, or in the neck and head of ribs, although the scarcity of epiphyses of long bones contributes to lower archeological visibility of these tasks in general. The same goes for skinning, inferred through cut marks on the skull and metapodials (Tables 6 and 7), since the remains of the former are fragmentary and the latter scarce. Cut marks related to skinning are located on the frontal, orbital, and nasal regions of the skull and on

| %MAU | LD | p   |
|------|----|-----|
| TD10.2 | 0.007 | 0.7  |
| MR | 0.007 | 0.7  |
| SC | 0.007 | 0.7  |
| HM | 0.007 | 0.7  |
| MC | 0.007 | 0.7  |
| IM | 0.007 | 0.7  |
| FM | 0.007 | 0.7  |
| TA | 0.007 | 0.7  |
| MT | 0.007 | 0.7  |

Table 3
Correlation coefficients between landmarks %MAU and landmarks volume density (VD) — linear density (LD). For abbreviations, see legend of Table 2.

| %MAU | Utility correlations r_s p Bootstrap 95% CI p   |
|------|-----------------------------------|-----------------|-----------------|
| TD10.2 | 0.073 | 0.7   | 0.0365 | 0.01265 |
| MR | 0.073 | 0.7   | 0.0365 | 0.01265 |
| SC | 0.073 | 0.7   | 0.0365 | 0.01265 |
| HM | 0.073 | 0.7   | 0.0365 | 0.01265 |
| MC | 0.073 | 0.7   | 0.0365 | 0.01265 |
| IM | 0.073 | 0.7   | 0.0365 | 0.01265 |
| FM | 0.073 | 0.7   | 0.0365 | 0.01265 |
| TA | 0.073 | 0.7   | 0.0365 | 0.01265 |
| MT | 0.073 | 0.7   | 0.0365 | 0.01265 |

Table 4
Correlation coefficients (Rho) and bootstrap regression/correlation (Spearman method) between %MAU and Food Utility Indices. MGUI (Binford, 1978); (S)FUI (Metcalfe and Jones, 1998); (S)AVGTP, (S)AVGFUI, (S)Marrow (Emerson, 1993); UMI (Morin, 2007); and MDI (Friesen, 2001).
Anthropogenic modifications located in the bison set of Gran Dolina TD10.2. The columns show NISP and frequency by anatomical element. Cut marks (CM), Percussion marks (PM) and Human tooth marks (HTM). For abbreviations, see legend of Table 2 except for VR: Vertebra, CP: Carpal, TR: Tarsal, and PH: Phalange, used to group elements.

| Element | CM (%) | PM (%) | HTM (%) |
|---------|--------|--------|---------|
| CRN     | 7      | 1.0    | 0.1     | 0       | 0.0    |
| MR      | 61     | 9.1    | 24.0    | 3.6     | 5.0    |
| IT      | 1      | 0.1    | 0       | 0       | 0.0    |
| HY      | 5      | 6.2    | 0       | 0       | 11.3   |
| VR      | 40     | 2.9    | 1       | 0.1     | 7.0    |
| RB      | 364    | 9.4    | 30.0    | 0.8     | 147.0  |
| SC      | 8      | 10.7   | 0       | 0       | 0.0    |
| HM      | 24     | 19.2   | 20.0    | 16.0    | 0.0    |
| RD/UL   | 35     | 41.2   | 19.0    | 22.4    | 0.0    |
| CP      | 1      | 1.9    | 0       | 0       | 0.0    |
| MC      | 16     | 16.8   | 16.0    | 16.8    | 0.0    |
| IM      | 17     | 22.4   | 1       | 1.3     | 0.0    |
| SA      | 1      | 4.8    | 0       | 0       | 0.0    |
| FM      | 23     | 34.8   | 16.0    | 24.2    | 0.0    |
| PT      | 0      | 0      | 0       | 0       | 0.0    |
| TA      | 32     | 36.4   | 16.0    | 18.2    | 0.0    |
| AS      | 1      | 33.3   | 0       | 0       | 0.0    |
| CA      | 0      | 0      | 0       | 0       | 0.0    |
| TR      | 0      | 0      | 0       | 0       | 0.0    |
| MT      | 14     | 18.4   | 14.0    | 18.4    | 1.3    |
| IMP     | 3      | 4.8    | 1       | 1.6     | 0.0    |
| PH      | 6      | 5.2    | 15.0    | 12.9    | 0.0    |
| IFL     | 155    | 1.9    | 4.0     | 0       | 14.0   |
| ILB     | 176    | 7.3    | 114.0   | 4.7     | 6.0    |
| Indet.  | 29     | 1.4    | 3       | 0.1     | 0.0    |

Total: 1019

-107 192

Figure 5. Correlation plot between anatomical representation (%MAU) and food utility indices: a) Marrow index (Emerson, 1993), b) Unsaturated Marrow Index (UMI) (Morin, 2007), and c) Correlation coefficient (Pearson) of high-survival anatomical elements (%MAU) and Standardized Food Utility Index (S)FUI (Metcalfe and Jones, 1988) for the bison from the TD10.2 bone bed (green dotted line) and for a hypothetical reverse bulk pattern (pink continuous line) (after Faith and Gordon, 2007). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 5

Each data element has been ascribed to a possible agent. Anthropogenic breakage is defined by percussion marks for ascribing the breakage to human activity, and green breakage for carnivores. The former can be related to other activities or to carnivore breakage. On the contrary, green breakage is mainly attributable to carnivores. The former is characterized by cracks, the presence of red marrow, and the subsequent fleshing of the bone. The latter is mainly related to the breakage of the cortical bone, which suggests that the bone was snapped during detachment from the vertebral column. The value of these features is higher in the frontal bone (Keeley, 1990; Pickering and Egeland, 2006; Pickering et al., 2013). The breakage of the phalanges, the skulls, and the long bones is significantly higher in the TD10.2 bone bed (green dotted line) and for a hypothetical reverse bulk pattern (pink continuous line) (after Faith and Gordon, 2007). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The bison-set preserves evidence of anthropogenic breakage by percussion and peeling on 390 specimens (NISP). The breakage involves both long and flat bones. The diagnostic features are related to the use of tools for percussion such as anvils, hammer stones, and choppers (NISP = 295) and with the bending of flat bones generating modification in the form of peeling (NISP = 95). Percussion bone breakage is mainly on bones with high marrow content (NISP = 216; 73%) (Table 5), being especially common on the femur and radius/ulna. Indeterminate long bones, numbering 114 specimens, complete the group (47% NISP). The location of percussion pits and notches on long bones can be seen in Figure 9. These are situated on the ends of the diaphysis, near the metaphyseal area. The pattern is repetitive on the ulnae, humeri, radii, and femora. Adhered flakes (NISP = 63) and conchoidal scars (NISP = 18) have also been observed. The bone flakes attributed to anthropogenic breakage amounted to 51, although another 956 with green fracture outlines have no diagnostic characteristics attributable to a particular agent. The abundant percussion breakage of long bones recorded in the set (and as discussed below, the few fractures of long bones attributed to carnivore activity), allow for the suggestion that many of these fragments are likely anthropogenic. In addition to the fracture of long bones, the intentional fracture of some elements with low medullary return, such as ribs and proximal phalanges, has been observed. On ribs, percussion fractures have been recorded on the costal angle area in 30 cases, as a means to access the inner red marrow (Binford, 1978; Pickering et al., 2013). Crushing and anvil damage on the opposite side and cracks extending from the area of percussion along the shaft have also been observed. There are two cases of large pits and large triangular depressions without internal micro-striation, which is associated with percussion by unmodified hammer stones and choppers (Domínguez-Rodrigo and Barba, 2006; Pickering and Egeland, 2006). However, ribs were broken mainly by peeling (NISP = 66). As shown above, 523 ribs fragments show features of green breakage. In the case of proximal rib fragments displaying spiral fractures (NISP = 74), archæological analogy suggests that these were probably snapped during detachment from the vertebral column (Hill, 2008) (Fig. 11).

In relation to the proximal phalanges, no diagnostic criteria were found in the form of percussion marks for ascribing the

the anterior side of metapodials. The skinning of the heads must be related to alimentary purposes (the exploitation of the brains) or with the extraction of the hides. Regardless of the aim of skinning the heads, the difficulty in handling and the high cost in terms of time and energy to remove the skin from the head (personal observation) indicates that, at least sometimes, hominins were interested in obtaining skinned skulls or the skull’s skin.

Other marks usually related to skinning are cuts on phalanges. On six different phalanges of the bison-set (four PH1 and two PH2), slicing marks have been observed and can be related to skinning of the shanks. However, on three PH1, the location and orientation of the cuts must be related to other butchering activities. As shown in Figure 10, oblique and longitudinal cuts on the distal articular surface can be related to disarticulation, possibly to facilitate breakage (see below).
fractures to hominin activity. However, the recurrence of the breakage pattern (30% of the PH1) consisting of longitudinally split PH1 which do not re-fit (Fig. 10), and the archeological and experimental parallels (e.g., Mateos Cachorro, 1999; Hill, 2008; Jin and Mills, 2011) point to an anthropogenic origin. In fact, the experiments of Jin and Mills suggest that “overall breakage pattern of the phalanges provide better evidence of human activities than percussion-generated surface modification” (op. cit: 1806), due to the fact that the breakage of disarticulated PH1 usually does not result in percussion marks. At least in some cases, as has been mentioned above, phalanges were effectively disarticulated.

Human tooth marks on the bison-set have been identified on 192 specimens (Table 5). They are predominantly located on ribs (76.3%) and, to a lesser degree, on unidentifiable flat bones (7.3%) and hyoids (5.7%), 48.4% of which are associated with other anthropogenic modifications, such as cut marks (Supplementary Online Material [SOM] Table S1). A large range of human tooth marks produced during the consumption of the carcasses have been characterized and recorded, although scored and pits are the most abundant. The basic statistics of the human tooth mark measurements are shown in Table 8. Metric values are close to experimental values obtained by Saladié et al. (2013a) (Fig. 12).

Finally, modifications have been documented on five long bone fragments that show impact marks due to their use as bone retouchers (Rodriguez-Hidalgo et al., 2013a) and, as in the whole

### Table 6

Description and quantification of the cut marks’ location and related butchering activities inferred from bison axial elements (plus scapulae and innominates) from the TD10.2 bone bed based on codes from Binford (1981: table 4.04), Nilssen (2000: table 4.37), and personal observations (ARH). Activities: SK: skinning, DS: dismembering, FI: filleting, EV: evisceration.

| Code | Part and description | Activity | CM |
|------|----------------------|----------|----|
| S-9  | Diagonal and transverse cuts on nasal and maxilla | SK | 4  |
| S-6  | Longitudinal cuts on maxilla above tooth row | DS | 3  |
| S-12 (ARH) | Diagonal cuts on frontal bone | SK | 1  |
| M-1  | Transverse cut on inferior surface of symphysis | SK | 1  |
| M-3  | Cuts on medial surface | DS (tongue) | 13 |
| M-10 | Cuts on lateral surface of area surrounding mental foramen | SK | 1  |
| M-4  | Cuts on the lateral face of retromolar space | DS | 1  |
| M5-7-9 | Cuts on inferior surface of mandibular condyle, medial, and lateral surface of the coronoid process | DS | 4  |
| M-11 | Cuts on lateral and ventral surface of the mandibular body and angle | SK | 34 |
| HY-1 (ARH) | Diagonal cuts on lateral and border of stylohyoid | DS (tongue) | 5  |
| TV-2 | Longitudinal and diagonal cuts along base and lower part of the dorsal spine | FI | 27 |
| TV-6 | Diagonal and transverse cuts on inferior surface of centrum | EV | 1  |
| TV-5-9 | Cuts on superior surfaces of centrum, ventral surfaces of articular, and transverse processes and ribs facets | DS (ribs) | 2  |
| LV-1 | Cuts on both sides of dorsal spine | FI | 2  |
| LV-3 | Cuts on dorsal and lateral surfaces of cranial process | FI | 1  |
| LV-4 | Cuts on dorsal surface of transverse process | FI | 1  |
| RS-2 | Distal ends of the ribs cut off | DS | 5  |
| RS-3 | Transverse cuts on ventral rib surface just to the side of the rib head | DS (ribs) | 12 |
| RS-4 (ARH) | Predominantly transversal and diagonal cuts on lateral surface, cranial and caudal border of the rib from tuberosity of intercostal muscle to medial diaphysis | FI | 229 |
| RS-5 (ARH) | Predominantly transversal and diagonal cuts on medial surface from costal angle of intercostal muscle to medial diaphysis | EV | 100 |

### Table 7

Quantiﬁcation of the cut marks’ location and related butchering activities inferred from bison long limb bones from the TD10.2 bone bed based on descriptions from Binford (1981), Nilssen (2000), and personal observations. For abbreviation of elements, see legend/key of Table 2. PE: Proximal epiphysis; S: Shaft; DE: Distal epiphysis. For abbreviation of activity, see legend/key of Table 6. PR: Periosteum removal.

| Element | Activity | NISP |
|---------|----------|------|
| HMPE    | –        | –    |
| MHIS    | FI       | 22   |
| MDHE    | DS       | 2    |
| RDPE    | DS       | 9    |
| RD5     | FI       | 17   |
| RDDE    | –        | –    |
| FMPE    | –        | –    |
| FMS     | FI       | 23   |
| FMDE    | –        | –    |
| TAPE    | –        | –    |
| TAS     | FI       | 30   |
| TADE    | DS       | 2    |
| MPPE    | –        | –    |
| MPS     | SK + PR  | 33   |
| MPDE    | –        | –    |
| PHPE    | –        | –    |
| PHS     | SK       | 1    |
| PHDE    | DS       | 1    |
sequence of Gran Dolina, neither burned bones nor other signs of fire have been recorded.

4.1.2. Carnivore activity In the bison-set, the activity of carnivores has been determined through tooth marks, carnivore breakage, and digested bones on 6.1% of the specimens (NISP = 1436). Pits, scores, and perforations (98.4%), furrowing (10.2%), and scooping-out (1.3%) have been observed. Sometimes, the tooth marks are numerous, generating pitting on 9.7% of the chewed remains. Other modifications associated with carnivore consumption of carcasses are licking (4.1%), crenulated edges (3.1%), crushing (1.7%), and saw toothed edges (1.2%). Elements fractured by carnivores (3.6%) and digested bones (1.8%) have also been identified (Table 9).

With respect to the NISP, no element or segment of the carcasses is especially affected by carnivore damage ranging in frequency although those showing the highest frequencies commonly have low marrow values (Table 10). It should be noted that anatomically indeterminate bison long bones, mainly shaft fragments, show a low frequency of carnivore tooth marks. The general frequencies with respect to bones chewed by carnivores show that ribs are the most frequently tooth marked (42.4%), followed by indeterminate flat bones (19.8%), vertebrae (9.6%), and indeterminate long limb bones (9.5%). The remaining elements show carnivore tooth marks in frequencies below 6% for most of the skeleton. Among the long limb bones, epiphysial and near epiphysial fragments showed marks more frequently than shaft fragments (24.8%, 18.1% vs. 6.2%) (Table 11, Fig. 9).

As previously stated, the less dense portions of long bones are scarce in the bison-set. The loss of the epiphysis may relate to the ravaging by carnivores (e.g., Marean and Spencer, 1991) as

Figure 6. Examples of cut marks from the TD10.2 bison set: a) slicing marks, b) scrape marks, c) chop marks, d) saw marks, and d) slicing marks images obtained through low vacuum SEM.

Figure 7. Frequency distribution of the cut marks along the bison skeletons in the TD10.2 bone bed. The different colors indicate the percentage values of cut-marked bones. Bison design modified after M. Coutureau © 2013 ArchéoZoo.org.
suggested by the distribution of modifications on these bone portions. Heavy furrowing affected 7% of the bones chewed by carnivores (0.6% of total of NISP). In four cases (two metacarpals, one femur, and one indeterminate long bone), scooping-out was observed. Pitting has been recorded mainly on ribs \((n = 42)\), flat bone fragments \((n = 28)\), and long bones \((n = 24)\).

The fractures attributed to carnivores have been identified by the presence of notches and perforations on the fracture edge. However, these modifications are scarce \((n = 52)\) and affect different elements, particularly ribs \((NISP = 11)\) and long bones \((NISP = 19)\) (Table 10). The presence of one tibia, one ulna, one femur, two metacarpals, and one metatarsal fractured by carnivores is noted. Other fracture morphologies, such as channeled fractures and crenulated edges (Binford, 1981), complete the group of carnivore modifications. Given that the notches are mostly on shafts and that the remains are of adult bison, the intervention of "bone crackers," such as wolf/dhole and hyenas, must be considered, although the latter have not been identified in the faunal assemblage. Traditionally in the European Middle Pleistocene, hyenas are strongly suspected, but there were also wolves capable of fracturing large mammal bones (Haynes, 1982). In fact, large canids (Canis lupus and Cuon alpinus europaeus) are the most abundant carnivores in the assemblage, and their remains are found in the bison bone bed.

Digested remains are scarce \((n = 26)\). Most are fragments of long bones or unidentified fragments that have been assigned to the bison group based on size. The few determinable pieces are sésamoids and fragments of teeth. Over 90% of the digested remains are moderately to heavily digested. The average length is 23 mm. No coprolites were found in the assemblage.

More than 1200 tooth marks have been measured. The mean of the width on cortical bones is 1.45 mm, while that on cancellous bone is slightly larger (1.95 mm). The maximum values for the width of perforation puncture and pit marks (7.3 mm on cortical bone and 8.69 mm on cancellous bone) clearly indicate the involvement of large carnivores with the carcasses. All metric

Figure 8. Location and distribution of cut marks (lines) and percussion marks (dots) on the limb bones of the bison from the TD10.2 bone bed.
parameters considered together suggest the involvement of large or and medium carnivores, such as large canids and hyenas (Table 12 and Fig. 12). However, we cannot dismiss the involvement of smaller carnivores, such as foxes, whose traces could be removed or marred by the signs of larger animals. In the same way, the involvement of large carnivores, such as bears, cannot be eliminated as a possibility. The combination of data on type, location, frequency, and intensity of gnawing with the measurements of tooth marks suggest that durophagous carnivores were responsible for some of the modifications recorded in the assemblage. The relative abundance of remains of large canids and the absence of remains of hyaenids and coprolites point to the former as the main carnivore bone modicators in TD10.2. Nevertheless, the intensity of some modifications and the large size of the bison carcasses also suggest the involvement of hyenas.

4.1.3. Co-occurrence of modifications and estimation of carnivore ravaging In the bison-set, 91 specimens show cut marks or anthropogenic bone breakage (percussion and/or peeling) and carnivore tooth marks (Table 13 and Figs. 13 and 14). The occurrence of human and carnivore modifications has been observed on long bones (0.5% NISP) and ribs and vertebrae (0.5% NISP). This very low co-occurrence suggests independence in the formation of the set, but this result may have been altered by the different distribution of damage along the portions of the bones (Saladié et al., 2014).

Carnivore tooth marks and cut marks overlap on seven remains. In all cases, carnivore marks are superimposed over the cut marks evidencing secondary access by the former (Fig. 14).

The results of the estimation of carnivore ravaging through taphonomic indices can be seen in Table 14. This indicates a
moderate to high ravaging when the indices that reflect the epiphysis to shaft ratios are considered and very light ravaging according to the axial to appendicular index. These results are contradictory because they indicate a strong loss of epiphyses of the long limb bones by carnivore ravaging that does not correspond to the expectation for the axial skeleton ravaging, which should be high. Nevertheless, the results are similar to other sites in which large ungulates predominate and these other sites have been interpreted as kill sites, as it must be supposed that whole carcasses are present prior to anthropogenic selective transport and carnivore ravaging (Fig. 15). These results suggest that when anthropogenic mass predation events of large ungulates occur, subsequent carnivore ravaging hardly affects the representation of the axial skeleton, probably due to its abundance in the complete skeletons. This seems to be the case in the TD10.2 bison bone bed.

4.2. Other taxa in the bison bone bed of TD10.2

Only about 1% of the faunal remains of the bison bone bed belong to other taxa (NISP = 357). The other 1327 remains have not been assigned to a specific taxon. Of these, only 25 specimens have been included in a weight size category. The others are totally indeterminable. Therefore, NISP is the index used to describe the general characteristics of the non-bison remains in this section. The most abundant taxon is rabbit (Oryctolagus sp.) (NISP = 58), followed by equids (NISP = 55), large canids (NISP = 61) (C. lupus

Figure 10. Examples of breakage patterns on bison first phalanges from the TD10.2 bone bed. The arrow indicates slicing marks on the distal articular surface of a first phalange: (a) posterior and lateral proximal surface of two second phalanges (b) related to disarticulation prior breakage.
NISP = 7 and *C. alpinus* NISP = 3), medium-sized cervids (*Cervus/Dama* NISP = 48), and Aves (NISP = 41). Other taxa are represented by fewer than 30 specimens. Carnivores are diverse and abundant in terms of NISP and MNI. The scarcity of individuals prevents mortality interpretations, although immature individuals are common throughout these species (Table 1).

The anatomical representation of all taxa is highly biased for ungulates (SOM Table S2), carnivores (SOM Table S3), and mesovertebrates (SOM Table S4). The macromammals, both ungulates and carnivores, are mainly represented by isolated teeth and small and compact bones of the feet. Due to the high bias in skeletal representation of these animals, the ratio between MNE and MNI is very high (Lyman, 2008) (SOM Tables S3 and S4). The mesovertebrates are represented by isolated remains in the case of small mustelids, beavers, and marmots and by long limb bones in the case of rabbits and birds. However, due to the excavation method employed in the TD10 level of Gran Dolina, the remains of mesovertebrates have artificial biases in anatomical representation that prevent an adequate interpretation of their skeletal profiles (see methods section). As a result, most of the inferences made about these taxa represent only a partial view of the original set (work in progress).

With regard to the modifications on bone surfaces, there is no anthropogenic activity, except on a radius shaft of a medium sized bird. This specimen shows three oblique striae on the shaft (SOM Fig. S1). These marks must be related to the manipulation of the wings, supposedly for feathers (Romandini et al., 2016). However, taking into account that it is only one specimen, these signs must be carefully interpreted.

By contrast, signs of carnivore activity are abundant (11.2%) and affect all taxa (Table 15). Preserved distal portions of the long bones of rabbits and birds, as well as the high proportion of tooth marked and digested remains of these two taxa (21%) and the absence of anthropogenic activity, indicate their origin is likely related to the activity of non-human predators, probably small terrestrial carnivores and birds of prey (Lloveras et al., 2008, 2009, 2012; Rodríguez-Hidalgo et al., 2013b). This interpretation should be considered as tentative until an extensive assessment of mesovertebrates of the TD10.2 bone bed (under preparation) is completed.

5. Discussion

The large concentration of archeological remains in the TD10.2 bison bone bed represents a thin, discrete archeostratigraphic layer in which no significant post-depositional processes have occurred. It is an in situ layer where hominins performed tasks related to subsistence, tasks that have been interpreted in this work through examination of the faunal record. In the same stratigraphic context, the upper part of TD10 sequence (named TD10.1) has previously been studied from a taphonomical perspective (Díez, 1993a; Rosell, 2001; Blasco, 2011; Rodríguez-Hidalgo, 2015; Rodríguez-Hidalgo et al., 2015). Carnivores or post-depositional processes have not been inferred as major contributors to the formation of the faunal accumulations in the upper part of the Gran Dolina in contrast to lower layers, such as TD5 or TD8 (Saladié, 2009; Blasco et al., 2011). In fact, all previous zooarcheological investigations focused on TD10 point to hominins as the main modifiers and virtually the only accumulators of macrofaunal remains together with other cultural debris (Díez, 1993b; Rosell, 2001; Menéndez, 2010; Blasco, 2011; López-Ortega et al., 2011; Obregón, 2012; Terradillos-Bernal and Díez, 2012; Rodríguez-Hidalgo et al., 2015). In this regard, not only the thousands of lithic artifacts recovered with the bones, but the large number and significance of anthropogenic bone modifications, the selection of prey (in species and season of death), the mortality pattern, and the anatomical composition presented here demonstrated that hominins were the main accumulators of the TD10.2 bison bone bed. In this sense, this archeological layer is

![Figure 11. Bison ribs from the TD10.2 bone bed. The white dot line and arrow indicate green fractures (spiral or peel) and cut marks. The white line indicates carnivore tooth marks.](106)

Table 8
Statistical parameters of the human tooth marks (pits and scores) by type of tissue documented in the TD10.2 bison-set.

|          | n   | Mean | IC -95% | IC +95% | Min.  | Max.  | SD      |
|----------|-----|------|---------|---------|-------|-------|---------|
| Pit length cortical | 165 | 2.10 | 1.92    | 2.28    | 0.46  | 7.35  | 1.16    |
| Pit width cortical  | 166 | 1.25 | 1.14    | 1.37    | 0.73  | 0.25  | 0.17    |
| Pit length cancellous | 13  | 2.79 | 1.58    | 4.00    | 7.29  | 2.00  | 0.54    |
| Pit width cancellous | 13  | 1.68 | 0.98    | 2.38    | 1.16  | 0.40  | 0.25    |
| Score width cortical | 206 | 0.75 | 0.67    | 0.83    | 4.19  | 0.58  | 0.06    |

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another example in the Gran Dolina sequence indicative of the importance of the cave as a point of attraction in the paleo-territory of the Sierra de Atapuerca and provides an opportunity to observe and shed new light on the subsistence behavior and social organization of European hominins during the Lower Paleolithic.

The distribution and frequencies of cut marks, percussion marks, and carnivore tooth marks on skeletons documented in this work reflect primary access to complete carcasses by hominins, as well as systematic butchering for intensive exploitation. The high frequency of cut marks on meaty long bones, with respect to bones that have little exploitable meat, and on the shaft portions vs. long bone distal ends, together with the frequency of tooth marks and percussion marks on mid-shaft long bones, are consistent with those observed in assemblages interpreted as proof of ancient hominin hunting (Marean et al., 2000; Domínguez-Rodrigo and Pickering, 2003; Rabinovich et al., 2008, 2012; Thompson, 2010; Thompson and Henshilwood, 2011; Valensi et al., 2013; Domínguez-Rodrigo et al., 2014). The recurrence observed in the butchering activities and the quantitative relevance of the bone accumulation support the following conclusions: 1) the anthropogenic origin of the bison bone bed, and 2) hunting as the mode of access to the bison carcasses in TD10.2.

This is fully consistent with other well-documented and thoroughly taphonomically investigated assemblages from the Middle Pleistocene, such as Bolomor, Cuesta de la Bajada, and Gran Dolina TD10.1 and Gran Dolina TD6 in Spain (Blasco, 2011; Saladié et al., 2011; Domínguez-Rodrigo et al., 2015; Rodríguez-Hidalgo et al., 2015) Schöningen in Germany (Voormolen, 2008; Starkovich and Conard, 2015; Van Kolfschoten et al., 2015) and Gesher Benot Ya‘aqov and Qesem in the Near East (Rabinovich et al., 2008; Stiner et al., 2009); in which hunting emerges as the main method to acquire animal carcasses. This evidence suggests that predation is

Table 9

| Carnivore tooth marks               | NISP | %    |
|-------------------------------------|------|------|
| Pits, Scores and Punctures          | 1413 | 98.4 |
| Furrowing                           | 148  | 10.2 |
| Pitting                             | 140  | 9.7  |
| Licking                              | 59   | 4.1  |
| Carnivore breakage                  | 52   | 3.6  |
| Crenulated edge                     | 44   | 3.1  |
| Digested                            | 26   | 1.8  |
| Crushing                            | 25   | 1.7  |
| Scooping out                        | 19   | 1.3  |
| Saw tooth edge                      | 17   | 1.2  |
the norm and not the exception during the Early to Middle Pleistocene.

In addition, the zooarcheological results presented here indicate an assemblage highly dominated by one taxon, the bison. Remains of at least 60 individuals have been identified as part of the bone bed, although it is possible that the total number of bison accumulated is noticeably higher with respect to the total extension of the original cave, possibly double the area currently preserved and excavated. This large quantity of specimens, elements, and individuals in just twenty centimeters of accumulation and the scarcity of remains of other ungulates point to an assemblage that is virtually monospecific in ecological terms and that does not fit the model of a natural trap (Martin and Gilbert, 1978; Oliver, 1989; Wang and Martin, 1993; Marder et al., 2011) or bone accumulations by carnivores (Kruuk, 1972; Skinner et al., 1986; Cruz-Uribe, 1991; Pickering, 2002; Egeland et al., 2008), both of which are more eclectic in their taxonomic representation (Fig. 16). By contrast, anthropogenic faunal accumulations can become monospecific or highly selective (species-dominated) either by ecological constraints or deliberate economic strategies, nuances which are difficult to determine archaeologically (David and Enloe, 1993; Mellars, 2004; Costamagno et al., 2006; Rendu et al., 2012).

Monospecific or species-dominated archeological assemblages are relatively common in Europe during the Upper Pleistocene (e.g. Gaudzinski and Turner, 1996; Gaudzinski, 2005), including Mauran (Farizy et al., 1994; Rendu et al., 2012), La Borde (Jaubert et al., 1990), Coudoulous I (Brugal, 1999), and Wallertheim (Gaudzinski, 1995) in which large bovids were the focus of hunters. During the Middle Pleistocene, this kind of archeological, single species-dominated assemblage is not common, but some examples exist, such as Cuesta de la Bajada and Schoningen (horse-dominated assemblages) (Voormolen, 2008; Domínguez-Rodrigo et al., 2015). All of these sites have been interpreted as kill-butchering sites, and

| Table 10 |
|---|
| **NISP and frequency of carnivore tooth marked specimens by anatomical element in the TD10.2 bison-set.** For abbreviation of elements, see legend/key of Table 2. |
| **Element** | **NISP** | **carnivore tooth marks** | **%NISP tooth marked** | **%NISP** | **carnivore breakage** | **%NISP** | **carnivore breakage** |
| CRN | 5 | 0.3 | 0.7 | – | – | – |
| MR | 48 | 3.3 | 7.1 | 2 | 3.8 | 0.3 |
| CRN/MR | 1 | 0.1 | – | – | – | – |
| IVR | 138 | 9.6 | 10 | 3 | 5.8 | 0.2 |
| RB | 609 | 44.2 | 15.6 | 16 | 30.8 | 0.4 |
| SC | 12 | 0.8 | 16 | 2 | 3.8 | 2.7 |
| HM | 13 | 0.9 | 10.4 | – | – | – |
| RD | 11 | 0.8 | 12.9 | – | – | – |
| UL | 11 | 0.8 | 24.4 | 1 | 1.9 | 2.2 |
| CA | 8 | 0.6 | 14.8 | – | – | – |
| MC | 17 | 1.2 | 17.9 | 2 | 3.8 | 2.1 |
| IM | 15 | 1 | 20.5 | – | – | – |
| FM | 6 | 0.4 | 9.1 | 1 | 1.9 | 1.5 |
| PT | – | – | – | – | – | – |
| TA | 8 | 0.6 | 9.1 | 1 | 1.9 | 1.1 |
| AS | – | – | – | – | – | – |
| CA | 1 | 0.1 | 9.1 | – | – | – |
| TR | 4 | 0.3 | 30.8 | – | – | – |
| MT | 7 | 0.5 | 9.2 | 1 | 1.9 | 1.3 |
| MP | 8 | 0.6 | 12.7 | – | – | – |
| PH | 23 | 1.6 | 19.8 | – | – | – |
| ILB | 136 | 9.5 | 5.6 | 11 | 21.2 | 0.5 |
| IFB | 285 | 19.8 | 3.5 | 9 | 17.3 | 0.1 |
| AR | 5 | 0.3 | 19.2 | – | – | – |
| Indet. | 54 | 5.2 | 2.5 | 3 | 5.8 | 0.1 |

| Table 11 |
|---|
| **Relative proportion (% quotient) between epiphysis, near epiphysis, and tooth-marked shaft specimens (NISP) of long bones (numerator) and NISP (denominator) by portion of the bison-set of TD10.2.** |
| **Long limb bones** |
| Epiphysis | 32/129 |
| Near Epiphysis | 56/310 |
| Shaft | 118/1912 |
| **%** | 24.8 |
| 18.1 |
| 6.2 |

| Table 12 |
|---|
| **Statistical parameters of the carnivore tooth marks (pits and scores) by type of tissue.** |
| **n** | **Mean** | **IC 95%** | **Min.** | **Max.** | **SD** |
| Pit length cortical | 1003 | 2.28 | 2.20 | 2.37 | 0.22 | 14.49 | 1.39 |
| Pit width cortical | 895 | 1.45 | 1.39 | 1.51 | 0.10 | 7.30 | 0.88 |
| Pit length cancellous | 246 | 2.75 | 2.54 | 2.95 | 0.45 | 10.86 | 1.62 |
| Pit length cancellous | 234 | 1.95 | 1.79 | 2.11 | 0.31 | 8.69 | 1.22 |
| Score width cortical | 517 | 0.82 | 0.77 | 0.88 | 0.05 | 6.82 | 0.65 |
| Score width cancellous | 76 | 1.42 | 1.17 | 1.67 | 0.17 | 5.36 | 1.10 |

| Table 13 |
|---|
| **Co-occurrence of modification by NISP and % in long limb bones (LLB), and vertebrae plus ribs specimens (VR + RB) in the bison set of TD10.2.** Specimen showing tooth marks (TM), specimen showing cut marks (CM), specimen showing peeling (PEEL). |
| **NISP** | **TM + CM** | **%** | **TM + PM** | **%** | **TM + PEEL** | **%** | **TM + CM and/or PM and/or PEEL** | **%** |
| TD10.2 Bison LLB | 3065 | 15 | 0.5 | 2 | 0.07 | 0 | 0.00 | 15 | 0.5 |
| TD10.2 Bison VR + RB | 11,011 | 53 | 0.5 | 0 | 0 | 2 | 0.02 | 51 | 0.5 |
| TD10.2 Bison whole set | 22,532 | 83 | 0.4 | 5 | 0.02 | 6 | 0.03 | 90 | 0.4 |
Figure 13. Co-occurrence of modifications inflicted by hominins and carnivores on a bison distal femur from the TD10.2 bone bed assemblage. The arrows indicate carnivore tooth marks concentrated along a heavily furrowed distal epiphysis (left) and percussion marks (impact and adhered flake) on the diaphysis near the epiphysis. The femur shows cut marks on the diaphysis.

Figure 14. Co-occurrence of modifications (cut marks and carnivore tooth marks) in the bison set from TD10.2 bone bed. Co-occurrences have been documented in (a) the same specimen and in few cases, (b, c, d) in specific over-imposed marks indicating secondary access to the carcasses by carnivores. Black arrows indicate cut marks and white arrows indicate tooth marks.
hunting is doubtless the method used to access the animal carcasses. In fact, many of these sites and others in the Caucasus (Baryshnikov and Hoffecker, 1994; Gaudzinski, 1996) and South Africa (Klein, 1989, 1999; Marean, 1997) show evidence of tactical hunting suggesting that around the world, at least from the second half of the Middle Pleistocene, hominins were capable of highly organized hunting behavior (Marean, 1997).

Taking into account the anthropogenic origin of the bison bone bed of TD10.2, its low taxonomic diversity can be explained only by anthropic decisions as to what to hunt or by the environmental availability of prey other than bison. Paleoenvironmental data do not reflect significant changes in terms of paleoclimate or in micro- and macrovertebrate paleo-communities throughout the TD10 sequence that could constrain the spectrum of prey (García-Antón/C19son and Sainz-Ollero, 1991; Blain et al., 2008, 2009; Cuenca-Bescós et al., 2011; Rodríguez et al., 2011). In fact, the presence of 100 remains of horses, deer, and roe deer mixed with the bison remains reveal the availability of other prey, even prey considered as high-ranked in Optimal Foraging Theory. These high-ranked prey, such as red deer, were the target of Paleolithic hunters in other periods of the Gran Dolina sequence, together with a broad spectrum of other prey (Blasco, 2011; Saladié et al., 2011, 2014; Rodríguez-Hidalgo et al., 2015). However, in the bison bone bed, butchering marks

| Assemblages       | Origin | Main size class | Competition | % Carnivore | % Change | EP:SH | Ratio (HP + RD): (HD + RP) | AX:LB |
|-------------------|--------|-----------------|-------------|-------------|----------|-------|--------------------------|-------|
| TD10.2 Bison      | ARQ    | LS              | –           | 4.5         | 62.8     | 0.23  | 0.22                     | 5.66  |
| TD10.1inf LS<sup>1</sup> | ARQ    | LS              | –           | 6.9         | 67.5     | 0.06  | 0.11                     | 0.125 |
| TD10.1inf MS<sup>1</sup> | ARQ    | MS              | –           | 5.2         | 75.2     | 0.08  | 0.33                     | 0.091 |
| TD6.2 LS<sup>1</sup>  | ARQ    | LS              | –           | 8.9         | 85.9     | 0.08  | 0                       | 0.7   |
| TD6.2 MS<sup>1</sup>  | ARQ    | MS              | –           | 5.9         | 81.6     | 0.03  | 4                       | 0.7   |
| Folsom AMNH<sup>2</sup> | ARQ    | LS              | –           | 0.09        | 6.2      | 0.63  | 0.81                     | 3.12  |
| Agate Basin Hell Gap Component<sup>3</sup> | ARQ    | LS              | –           | –           | –        | –    | 0.13                     | 3.43  |
| Schöningen 131-4<sup>4</sup> | ARQ    | LS              | –           | 16          | 50.2     | 0.24  | 0.36                     | 4.45  |
| Syokimau TM<sup>5</sup>  | ACT    | SS-MS Low       | –           | 27.2        | 56.4     | 0.45  | 0.18                     | 0.27  |
| Amboseli (Kenya)<sup>6</sup> | ACT    | SS-MS Low       | –           | –           | –        | –    | 39.28                    | 3.08  |
| SelvHR<sup>7</sup>    | ACT    | SS-MS High      | 65          | 65          | 65       | 0.02  | 0.67                     | –     |

<sup>1</sup> Unpublished data of the corresponding author; (1) Saladié et al. (2011); (2) American Museum of Natural History (data from authors); (3) Hill (2008); (4) Voormolen (2008); (5) A. Egeland (2008); (6) from Faith and Behrensmeyer (2006); (7) from Selvaggio (1994b) (highly ravaged assemblage). (ARQ) Archeological; (ACT) Actualistic; (LS) Large size; (MS) Medium size; (SS) Small size. Ratio epiphyses to shafts (EP:SH), ratio proximal humerus (HP) plus distal radius (RD) to distal humerus (HD) plus proximal radius (RP), and ratio axial (AX) to limb bones (LB).

Table 15

NISP and frequency of carnivore tooth marks, digestion and carnivore breakage on the non-bison set recovered in TD10.2 bison bone bed.

| Carnivore tooth mark (%) | Digested (%) | Carnivore fracture (%) |
|--------------------------|--------------|------------------------|
| Oryctolagus sp.          | 22 (37.9)    | 11 (18.9)              |
| Equus sp.                | 4 (7.3)      | 1 (1.8)                |
| Canidae indet. Canis/Cuon cf. | 3 (5.9)    | 1 (2.0)                |
| Cervus elaphus/Dama dama clactoniana | 5 (10.4)  | 7 (14.6)               |
| Aves                     | 7 (17.1)     | 1 (2.4)                |
| Vulpes vulpes            | 2 (6.9)      | 1 (3.4)                |
| Castor fiber             | 3 (18.8)     | 0 (0)                  |
| Panthera leo spelaea     | 0 (0)        | 0 (0)                  |
| Carnivora indet.         | 1 (11.1)     | 1 (11.1)               |
| Lynx sp.                 | 0 (0)        | 0 (0)                  |
| Canis lupus              | 0 (0)        | 0 (0)                  |
| Marmota marmota          | 0 (0)        | 0 (0)                  |
| Capreolus priscus        | 1 (25)       | 0 (0)                  |
| Mustelidae indet. Meles meles | 0 (0)      | 0 (0)                  |
| Cuon alpinus             | 0 (0)        | 0 (0)                  |
| Erinaceus europaeus      | 0 (0)        | 0 (0)                  |
| Hystric sp.              | 0 (0)        | 0 (0)                  |
| Mustela putorius         | 0 (0)        | 0 (0)                  |
| Testudo hermanni         | 0 (0)        | 0 (0)                  |
| Indeterminate            | 29 (2.2)     | 3 (0.2)                |
| Total                    | 83           | 44                     | 33         |
bison remains indicate the presence of large and small carnivores inside the cave, scavenging the bison carcasses and probably occasionally introducing some elements of their prey and their own skeletons. Among abiotic processes, the fortuitous inclusion of small elements, like isolated teeth, phalanges, and articular bones, by gravitational and water flow transport into the bison bone bed cannot be dismissed as reflected by a small percentage of rounded bones concentrated along the water surface channel described above. Thus, the taphonomy and anatomical composition of the non-bison remains of TD10.2 suggest that the accumulation is a palimpsest like most Pleistocene cave deposits. Although all of these features indicate different taphonomic pathways for the two sub-sets analyzed in this work, the background noise provides the opportunity to observe the environmental diversity and the availability of other prey surrounding the cave during formation of the bone bed. The presence of at least 20 macromammal taxa in the assemblage indicates a broad spectrum of animal resources. However, these taxa were not exploited by hominins, at least during the events related to deposition of the bison remains. This indicates that the exploitation of a single taxon was a deliberate decision and permits a discussion of an acquisition strategy focused on bison hunting.

In addition to this prey selection, mortality data suggest the development of mass procurement at TD10.2. Mass procurement or multiple predation is defined as the procurement of more than one prey during a single hunting episode developed in a short period of chronological time (Steele and Baker, 1993; Driver, 1995; Lubinski, 2013). This kind of hunting strategy is performed exclusively by humans when the prey is large vertebrates (Steele and Baker, 1993), and it is broadly documented in both ethnographical and ethno-historical contexts (for a review see Forbis, 1978). The best-known archeological cases are in the context of communal bison hunting on the North American Great Plains (e.g., Frison, 2004; Meltzer, 2006) and in the context of reindeer hunting in Western Europe during the Upper Paleolithic (e.g., Enloe and David, 1997; Enloe, 2003), both carried out by groups of anatomically modern humans.

One of the main lines of evidence used to infer multiple predation resides is the mortality data (Frison and Reher, 1970; Reher and Frison, 1980; Lubinski and O'Brien, 2001; Rendu et al., 2012; Lubinski, 2013). The mass kill events generate catastrophic mortality profiles in which the frequency of individuals is inversely proportional to their age (Reher, 1970, 1973; Stiner, 1991). In addition, the simultaneous death of several individuals in a herd can be inferred through various methods, which in turn allows for the determination of the presence of seasonal mortality (Burke and Castanet, 1995; Todd et al., 1996; Aaris-Sørensen et al., 2007; Rivals et al., 2009). In TD10.2, three independent lines of evidence were observed to assess the structure of mortality and the seasonality of death for the bison population. The convergence of results obtained by the eruption, wear, and dental micro-wear indicates that most of the bison were slaughtered during two restricted seasonal windows in the late spring and early fall (Rodríguez-Hidalgo et al., 2016). While this confirms that the site was used intensively at least two times, taking into account the differential statistical results of tooth microwear compared with long and short-term occupations (Rodríguez-Hidalgo et al., 2016), it can be surmised that the site was used recurrently more than twice, perhaps over a few generations, similar to other archeological well-known kill sites (Reeves, 1978a, 1990; Reher and Frison, 1980; Wilson, 1980). A conclusion of recurrent and generational use does not necessarily mean that the site was occupied or associated with events of mass predation each year or each season during a geologically extended or chronologically very extended period, as, if this was the case, the number of accumulated individuals would be expected to be in the hundreds or even thousands, as proposed.
for Mauran (Farizy et al., 1994) and Coudoulous I (Brugal, 1995) in France, and Vore Buffalo Jump in Wyoming (Reher and Frison, 1980). The limited number of individuals in the TD10.2 bone bed suggests that perhaps the site was visited and used only once during the life of an individual (hunter) according to the ethnohistoric record of hunter-gatherers’ land use and the use of kill sites in communal hunting (Binford, 1978, 1983; Speth, 1997; Kelly, 2013). Seasonal mortality peaks at TD10.2 could correspond to stratigraphically overlapped events of several individuals. These events probably were performed at or near the site by one band of hominins with a common cultural tradition with some intra-seasonal variation, perhaps following the migration cycles of the bison herds. In this sense, the mortality structure of the bison remains at TD10.2, similar to an extant population, supports the hypothesis of mass/multiple predation events of larger or smaller groups of bison and refutes the hypothesis of single predation in which only one prey individual is captured, a hunting technique that usually produces prime dominated mortality profiles (Bunn and Pickering, 2010; Stiner, 2013; Bunn and Gurtov, 2014). The broad representation of calves and yearlings in the assemblage, animals that are only part of larger groups of mixed (or cow) herds (Speth, 1997; Lott, 2003; Krasinska and Krasinski, 2007), reinforces the living population structure of the mortality events and the possible targeting of cow herds. Nevertheless, the nature and objective of the kills can differ seasonally (Speth, 1997), and the hominins of the Sierra de Atapuerca could have hunted different kinds of herds, such as small cow herds during the warm season and larger herds during the rut season. Currently, it is impossible to differentiate between the bones that correspond to each seasonal peak in the study assemblage.

Along with mortality data, the selection of prey evidenced in the taxonomic composition, the taphonomic features of the bison remains and anatomical data discussed below makes overlapping mass predation events the most plausible explanation for the accumulation of the TD10.2 bone bed. According to the classification of Bailey (2007), the bone bed is a cumulative palimpsest in which some evidence has been deposited over other evidence. Such deposits are less useful in behavioral inferences because of mixed contributions. However, the characteristics of the TD10.2 bone bed indicate that the same activity involving hominins and bison was repeated in several episodes. This overlap of similar events leads to a greater interpretive power for the assemblage.

The extensive identification of tasks associated with the early stages of the butchering process and the abundance of anatomical elements that are typically infrequent in Paleolithic sites, such as hyoid, ribs, and caudal vertebrae, in the TD10.2 bison-set allow for the consideration of use of the cave itself and its immediate surroundings as a place for the procurement and processing of carcasses. Despite the large variation observed in the butchering patterns and the sequence of consumption of carcasses by humans (Gifford, 1977; O’Connell et al., 1992; Domínguez-Rodrigo, 1999), some gestures and activities are recurrent in part due to anatomical and carcass size constraints and provide the opportunity to interpret the butchering process by analogy (Binford, 1981; Nilssen, 2000). As Hill (2008) notes, one of the first butchering tasks developed at bison kill sites is the extraction of the tongue, an organ rich in fat (McHugh, 1972; Wheat, 1972, 1979; Lupo, 1998; Hill, 2008). After removal, the tongue could be consumed as a snack at the kill site together with the marrow of the long bones and mandibles (Binford, 1978; Bunn and Kroll, 1988). In the assemblage presented here, cut marks on hyoids are from the internal surfaces of mandibles indicate the exploitation of bison tongues. The frequent representation of hyoid in the assemblage can also be related to the recurrent consumption of tongues in situ, inferred by the presence of human tooth marks. If this interpretation is correct, the discarded hyoid bones would have been of little interest to scavengers because no marrow or other tissues were present and would favor the exceptional survival of hyoid bones in the bison-set at TD10.2. The alternative explanation is that the tongues were removed in situ and stripped of the hyoids to be transported to the site, even if Gran Dolina was the primary kill site or the secondary butchering site. However, regardless of which scenario occurred, the TD10.2 assemblage provides valuable information concerning one of the less documented butchering activities during the Paleolithic, the exploitation of the tongue, due to the scarcity of hyoid bones in the fossil record.

One of the most extensively documented early butchering tasks in the TD10.2 bison-set is evisceration. Cut marks related to thoracic visceral removal are typically infrequent at Pleistocene sites due to the scarce representation of ribs in the assemblages (Marean and Cleghorn, 2003). By contrast, the 3892 costal specimens in the TD10.2 bison-set, more than 360 rib fragments display cut marks, and 100 of them are related to visceral removal. This task is developed invariably at a kill site when large ungulates are involved (O’Connell et al., 1992; Lupo and O’Connell, 2002). Gutted trunk portions can be transported to the camp site and this is a common practice for large prey, such as bison (O’Connell et al., 1980; Emerson, 1993). However, the high number of ribs present in the bone bed suggests that the trunks were originally complete in the cave. In the bison-set, ribs also show intensive processing, usually being disarticulated to facilitate their exploitation. The recurrent breakage of ribs generates a standardized pattern comparable to those observed in North American bison kill-butchering sites (Hill, 2008; Fig. 4.16). Such standardization may be related to the reduction of carcasses into more manageable packets (personal observation) and the consumption of red marrow, which is rich in unsaturated fatty acids. This kind of consumption has been ethnographically recorded among the San (Yellen, 1977), Hadza (O’Connell et al., 1988; Hawkes et al., 1991; Lupo and O’Connell, 2002; Marlowe, 2010), and Nunamiat (Binford, 1978) within kill/butchering sites as part of snacking, but with the important difference of roasting and/or boiling the ribs before consumption. It is possible that the percussion breakage documented in the costal angle of the ribs in TD10.2 can be related to the extraction and exploitation of red marrow without pyro-technology. Modern experiments show how easy it is to break the costal angle of the ribs with hammerstone percussion, and the amount of red marrow included in this portion of the skeleton (personal observation) is much more than is present in phalanges, which were frequently exploited at prehistoric sites. In the TD10.2 bison bone bed, ribs also display abundant human tooth marks, which, together with the abundant cut marks, peelings, and breakage by percussion, strengthen the interpretation of intensive exploitation of carcasses and on-site consumption of parts of the carcasses as snacks during the butchering process.

Finally, among the butchering activities supposedly developed in the early stages of the butchering process, skinning has been documented in the bison bone bed. It is inferred that skinning took place according to a systematic and recurrent pattern comparable to that performed by the Nunamiat (Binford, 1978, 1981), various Native American groups (Prison, 1971; Wheat, 1979), and modern butchers (Nilssen, 2000; personal observation). Careful skinning of heads and phalanges, although there are scarce remains and fragmentary representation, indicates that meat and fat were not the sole targets of the economic activities developed in the bone bed, as much of the equipment used by late Middle Pleistocene humans, including clothing, shelter, sleeping gear, and transport containers, was probably formed from skins. Direct evidence of these activities was provided by the preliminary use-wear analysis of the stone tools, where hide-working involving hafted chert endscrapers was
inferred (Márquez et al., 2001). Certain elements, such as the caudal vertebrae, are significant in this regard. On one hand, the presence of caudal vertebrae is direct evidence of at least some carcasses arriving in the cave unskinned and possibly in their complete form. On the other hand, their relatively low representation can be indicative of the exploitation of hides, as has been recently proposed in the Schöningen spear-horizon level (Conard et al., 2015). However, a lack of caudal vertebrae can also correspond to the transport of a majority of the skins and a large number of attritional phenomena that may affect these small remains.

The data presented here support the anthropogenic origin of the bone bed accumulation in the form of overlapping seasonal events of mass procurement of bison herds. Although some of the activities documented extensively in TD10.2 can be related to the early stages of the butchering process, it is difficult to establish whether the bison carcasses were transported to the cave from the kill site or the cave itself functioned as the kill-butchering site.

Traditionally in zooarcheology, the anatomical profile is considered as primary line of evidence in the assessment of the functionality and character of occupations. However, the significance of the skeletal representation is relevant to the establishment of behavioral inferences since the formation of Paleolithic assemblages is conditioned by a large number of stochastic variables that are involved in decisions concerning transport (Bunn and Kroll, 1988; O’Connell et al., 1988, 1990; Bunn, 1993; Gifford-Gonzalez, 1993; Monahan, 1998; Schoville and Otárola-Castillo, 2014) and by the wide variety of agents and processes that can be involved in the final configuration (Lyman, 1984, 1985; Grayson, 1989; Marean and Spencer, 1991; Marean et al., 1992; Morlan, 1994; Cleggorn and Marean, 2004; Faith et al., 2007). Skeletal parts or bone portions with low mineral density suffer more destruction (and are less represented) than those with high mineral density, especially if there is carnivore involvement. Thus, low-survival elements (lacking thick non-cancellous cortical portions) have been proclaimed as unhelpful in behavioral analysis (e.g., Marean and Cleggorn, 2003). Nonetheless, under certain circumstances, large ungulate remains can prevail at kill sites and butchering spots (O’Connell et al., 1992), especially ribs (Monahan, 1998), which can survive even heavy anthropogenic damage (O’Connell et al., 1992; Dominguez-Rodrigo and Martí, 1996) and carnivore consumption (Kruuk, 1972; Haynes, 1982; Dominguez-Rodrigo, 1999; Fosse et al., 2012; Gidna et al., 2014; Sala et al., 2014; Pobiner, 2015). Paradoxical high survival of low-survival elements is recurrent in sites where mass predation is the predominant hunting technique (Frison, 1974, 1978, 1987, 2004; Reher and Frison, 1980; Frison and Todd, 1987; Todd, 1987; Todd et al., 1997; Hill, 2008; Bar-Oz et al., 2011). At these sites, especially those where large prey are targeted, the amount of exploitable biomass far exceeds the immediate needs of the group, which results in an abandonment of important portions of carcasses at the kill site (Reher, 1970; Wheat, 1972, 1978; Frison et al., 1976; Stanford, 1978; Reher and Frison, 1980; Frison and Todd, 1987; Todd, 1987; Meltzer, 2006; among others). The high representation of trunks in mass death events (it is obvious that a complete skeleton has many more vertebrae and ribs than humeri) favors their survival despite their propensity to disappear from the record, even if the carcasses were subsequently scavenged by carnivores. Notwithstanding the carnivore ravaging observed in TD10.2, the anatomical profile shows a significant predominance of the axial skeleton, confirming the high survival of skulls, mandibles, hyoids, ribs, and vertebrae. This high survival rate of ribs and vertebrae allows for important behavioral inferences that are not only derived from the great quantity of taphonomic information presented in these remains, but also directly from the abundance of the set, which suggests that the bison were probably obtained close to the cave itself and processed prior to further transport. The high proportion of vertebrae and ribs relative to other skeletal elements, together with the evidence in the seasonality data of the slaughter of several individuals in each hunting event, shows a high representation of postcranial axial elements, considering that these elements disappear easily and are more difficult to estimate in MNE due to the scarcity of landmarks. Simultaneously, the very low representation of long bones must, therefore, be the result of subsequent transport since the activity of carnivores would not have significantly affected the diaphyses of these bones (Marean et al., 1992; Blumenschine and Marean, 1993). The random distribution of remains prevents the consideration of a hypothetical concentration of limb bones in any unexcavated part of the paleo-cave. This lack of long bones, including metapodialis, indicates the importance of not only meat, but also marrow, in the economic decisions of the hominins that generated the assemblage. This conclusion is further confirmed considering that long bones are the main anatomical parts representing bison-sized animals in the top level of TD10 (sub-layers TD10.1-upper portion-, and TD10.1 bone bed, both of which have been interpreted as residential camp sites) (Rosell, 2001; Rodríguez-Hidalgo, 2015). Regarding the exploitation of unsaturated fats, the breakage of the first and second phalanges noted in the bison bone bed has been claimed traditionally to be a sensitive indicator of nutritional stress (see Binford, 1981; Hodgkins et al., 2016). This does not seem to be the case in TD10.2, where nothing indicates famine, starvation, or nutritional stress. In this study, the lack of phalanges, the moderate to high incidence of carnivore ravaging, and the transport of the limbs away from the site, makes it difficult to assess the real impact of hominins and scavengers on the under-representation of the foot bones.

To explore further the meaning of the anatomical representation and its relationship with the function of the site, the TD10.2 assemblage can be compared to Paleoindian, Late Prehistoric, and historic faunal assemblages from the North American plains. Over ten millennia, different North American cultural groups developed the practice of communal bison hunting as part of their economic and social systems (Reher, 1970, 1973; Wheat, 1972, 1978, 1979; Schaeffer, 1978; Stanford, 1978; Wilson, 1978; Wilson and Davis, 1978; Frison, 1978, 1987, 2004; Reeves, 1978a, 1978b, 1990; Reher and Frison, 1980; Speth, 1983; Niven and Hill, 1998). This provides a large quantity of data concerning anatomical representation on which to draw analogies between the communal mass hunting of bison developed by Amerindian groups and the TD10.2 assemblage-analogies that are impossible to make with European Middle Pleistocene assemblages due to the scarcity of detailed anatomical data.

Bridging the spatiotemporal, cultural, and ecological gap, the bison-set of TD10.2 shows a similar skeletal profile to many sites characterized as kill sites or kill-butchery sites, especially those dating to late prehistoric and historic periods, in which there is an inverse relationship between food utility and representation. It is true that variability is important since many factors can influence the decisions taken by butchers from obvious variables, such as the number of animals slaughtered, to more subtle variables, like the weather at the time of the kill (Frison, 1974; Speth, 1997, 2013). This variability is also seen in TD10.2, where occasionally some elements of high-nutritional value, such as femora and humeri, were left in the cave after the full exploitation of their external and internal nutrients, while the norm seems to have been to transport them away from the cave (or leave them in the original kill if Gran Dolina was only a butchering camp). In the same way, the removal of some axial elements to other places cannot be eliminated as a possibility. This variability in transport decisions and the heavy carnivore ravaging observed in the TD10.2 bison bone bed could be the cause of ambiguity in food utility or the weak correlation between utility and representation. However, the activities performed
and carcass transport decisions were apparently stable enough to generate a reverse bulk utility curve, which is distinctive of ethnographic and archeological kill sites (Binford, 1978; Boyle, 2000; Enloe, 2004). When the high-survival elements are considered, the skeletal profile observed in TD10.2 is close to other kill sites that were heavily ravaged by carnivores, documented in both the ethnographic literature (Binford, 1978) and archeological excavations of sites such as Casper (Frison, 1974) and the Main Hell Gap Component at Agate Basin (Hill, 2008) (“Brevester site”) (Fig. 17). In this sense, the most plausible hypothesis is that the bone bed corresponds to the use of the cave itself as a kill-butchering site, but other possibilities cannot be totally dismissed (see below).

In order to explore a “holistic approach” (in the words of Gaudzinski-Windheuser and Kindler, 2012) to provide a picture of the social organization of the subsistence of hominins of Gran Dolina, we turn our zooarchaeological attention to the lithic assemblage associated with the TD10.2 bison bone bed. As mentioned above, there is a striking supremacy of chert with respect to other materials locally available, with no parallel in the other Atapuerca sites and layers. The assemblage composition clearly points to the existence of complete knapping sequences, that is, to the transport of abundant chert nodules and cores, which were exploited there, to the cave, in order to obtain flakes and a variety of retouched tools. This transport fits with a planned strategy to meet the needs for certain needs (e.g., the processing of several carcasses). Interestingly, among the few objects made from materials other than chert (quartzite and sandstone), some tool groups stand out: fluvial cobbles used as hammerstones for lithic production (and probably also for bone breakage) and large shaped tools, including handaxes and cleavers. This reinforces the idea of a planned behavior, especially if we take into account that the latter represent curated tools that seem to have been produced elsewhere (as characteristic items resulting from their production process are totally absent in the archeological set). According to personal experimental observations, the recorded stone tool kit is unquestionably sufficient to carry out the whole butchery process (from skinning to evisceration, disarticulation, defleshing and bone breakage), as well as some additional activities such as the hide processing revealed after the preliminary usewear studies.

Regarding the modes of foragers to cope with anticipated demands for tools, the TD10.2 assemblage seems to fit with what Kuhn defines as a provisioning of places strategy (Kuhn, 1995). This would ensure “a supply of raw materials and/or tools at the places where the activities will occur” (Costamagno et al., 2006: 468), and involves a prior knowledge of both the timing and the location of future activities (Kuhn, 1995).

The overlapping of different seasonal hunting events in the same spot, the involvement of large groups of hominins in the butchering tasks, and staying in the site, presumably for several days, to meet the goal of the hunting events would explain the features of the lithic assemblage, supporting the interpretation of the site as a kill-butchering spot. However, estimating in detail the duration of the occupations and their possible overlapping, as well as the role of some curated tools, will require the results from refitting and spatial studies that are currently ongoing.

Considering multiple predation to be the most likely technique of hunting developed at the Gran Dolina TD10.2 bone bed, and the probable use of Gran Dolina as a kill-butchering site, the transport of high-utility elements and a significant amount of meat, fat, and marrow to somewhere outside the cave implies high-energy expenditure and delayed consumption of the carcasses at a residential camp, with subsequent distribution of food among group members. This has been proposed at other sites of similar and older chronologies (Stiner et al., 2009; Saladie et al., 2011). In addition to food, other animal resources, especially hides, could be transported to other locations for handling and use. In turn, other alternative hypotheses, such as, the cave was a secondary butchering camp, also imply high-energy expenditure and delayed consumption of the carcasses at a residential camp, with subsequent distribution of food among group members. If our hypothesis that the TD10.2 bison bone bed represents the superposition of several (probably more than two) multiple predation events conducted at the same kill-butchering site is correct, data obtained in this research indicate that the amount of meat and other profitable animal resources accumulated in each of the kills would be formidable. In consequence, these hypothetically large quantities of hide, meat, fat, and marrow available after every mass-kill event would require a great deal of energy for their processing and transport. In this sense, tasks related to handling, butchering, and transportation must have been performed in a coordinated manner by numerous individuals, as has been described in historical sources recounting mass predation events of bison, reindeer, and seal (Wheat, 1972; Frison, 1978; Speth, 1997). Modern experiments suggest that it is necessary to coordinate work and that a large number of people (up to 10) are needed to systematically butcher a single adult bison carcass (personal observations). Furthermore, if multiple predation events are assumed, other economic options, such as transporting high-quality parts to caches, cannot be ruled out since communal hunting can contribute to the accumulation of resources in anticipation of times of scarcity (Binford, 1978; Driver, 1990) even though the production of a surplus is not a universal reason for communal hunts (Driver, 1990) and the question of whether Lower Paleolithic hominins preserved food is entirely moot (White et al., 2016). In fact, this research (especially the over-representation of ribs) does not suggest meat drying was of central importance. Finally, it is possible that the food provided by each predation event could be consumed completely by a large group, as occurs in other contexts of mass predation in which the social impact of the hunting events is more relevant to the people than its economic return in subsistence terms (e.g., Todd, 1987).

Figure 17. Correlation coefficient (Pearson) of high-survival anatomical elements (% MAU) between the bison set from the TD10.2 bone bed and the Casper site (CRS) (Frison, 1974), Nunamiat caribou kill sites (NUK) (after Binford, 1978), and Agate Basin Main Hell Gap Component (ABHG) (Hill, 2008).
In addition to the coordination and cooperation necessary for the processing and transport of carcasses, it is common for group members to cooperate and coordinate for participation in the mass procurement events themselves (Forbis, 1978; Frison, 1987; Speth, 1997, 2013). Not only the number of prey, but the number of participants in hunting events must be taken into account to differentiate between multiple predation, sequential predation, cooperative hunting, and communal hunting (Driver, 1990, 1995; Steele and Baker, 1993). From an anthropological point of view, Driver (1995) defines communal hunting as a practice in which a large number of group members, in particular individuals who do not usually hunt, are involved in hunting, distinguishing it from cooperative hunting in which several regular hunters coordinate on a hunting foray (Driver, 1990, 1995). Cooperative hunting has been proposed by several researchers to illustrate the early access to the carcasses of formidable prey, such as large bovids, horses, and pachyderms, by pre-modern humans without modern hunting weapons (Bratlund, 1999; Voormolen, 2008; Saladie et al., 2011; Dominguez-Rodrigo et al., 2014; Yravedra and Cobo-Sánchez, 2015; White et al., 2016). In the case of the TD10.2 bison bone bed, it is difficult to establish the form of hunting since it involves the study of extinct hominids. However, the intensity of exploitation of the carcasses and the large quantity of products transported in every possible kill event suggest the involvement of numerous groups of people in hunting and subsequent butchering, providing enough evidence to conclude that Lower Paleolithic hominins at Atapuerca were capable of developing tactical hunting strategies and techniques to communally hunt bison. It is true that it is very difficult to assess if some or all members of a Lower Paleolithic community were occasional or regular hunters. Nevertheless, our data on mortality, seasonality, skeletal profiles, taxonomic diversity and taphonomy support at least two overlapping mass predation events in which a large number of people had to participate.

Ethnohistorical and archeological sources indicate multiple techniques and methods for a successful mass kill (Gallardo, 1910; Furlong, 1912; Steward, 1943; Taylor, 1972; Santiago and Salemme, 2016). In the case of communal bison hunting, hunting parties can employ various techniques developed for the given circumstances and take advantage of a variety of both natural (streams, game jumps, cliffs, sink holes, sand dunes) and artificial (corrals, hunter stones) elements (McHugh, 1972; Forbis, 1978; Reeves, 1990; Speth, 1997; Frison, 2004). The methods used to drive the herds to the kill site are also diverse, but in all cases they require a high degree of organization, planning, coordination, and knowledge of prey by a large group of hunters and beaters (the last role often played by women and children) (Speth, 1997, 2013). Furthermore, the number of bison killed in a single event varies from dozens (the most common events) to several hundred (tends to have occurred only in recent periods).

Inferring the technique or techniques used at TD10.2 is a highly hypothetical but, the possibility that the paleomorphology of the cave and its location at the slope of the hill, could be used to drive the bison herds into a location where they would be more vulnerable cannot be eliminated as a possibility. As White et al. (2016) note, a cattle herd is easily driven to a desired point via the twin principles of the “point of balance” and the “flight zone” (White et al. 2016:7), but driving bison is more difficult (e.g., Lott, 2003). Nevertheless, following Bash and Marlor (2003:583), the hominins of Gran Dolina “could have learned to drive bison by trial and error. They could have observed bison over time, made systematic inferences about the nature of bison perception and cognition, and derived theories about manipulating bison behavior from models of bison psychology in a deductive ‘scientifc’ approach”.

Apart from Gran Dolina, there are several landforms in the area that could have been an advantage to a well-coordinated group of hunters (Speth, 1983, 1997; Olsen, 1989, 1995; Frison, 1998), including a narrow valley less than 150 m from Gran Dolina (Valle de la Propiedad) and limestone escarpments, such as the entrance of Cueva Mayor, less than 500 m from the cave. In fact, the possibility of the construction of perishable structures, like drivelines of stone carins (Friesen, 2013), to help guide the herds to Gran Dolina or other topographic traps near the cave cannot be rejected, as the capacity to construct structures seems to be much older than previously thought (Jaubert et al., 2016). These structures would have trapped the animals, causing them to be more exposed to hunters armed with throwing stones, stone tools, and maybe weapons such as wooden spears (Thieme, 1997). An example of this type of trap is seen at the penenecontemporaneous archeological site of Galería, 50 m away from Gran Dolina (Huguet et al., 2001). The site is a vertical natural trap that was used by hominins to access the carcasses of animals that had accidentally fallen into the cave pit (and was recurrently used for 200 kyr). The possibility that hominins knew the natural trap dynamic and were able to force or drive single animals into the sinkhole should be considered. In fact, the observation of the natural trap dynamic in Galería and other karstic natural traps has been hypothesized previously by the Atapuerca Research Team and collaborators for the Middle Pleistocene origin of communal-drive techniques developed by Neanderthals in the Upper Pleistocene (Brugal et al., 2006).

It is difficult to know whether the techniques used during bison accumulation events in TD10.2 were similar or comparable to communal hunting techniques developed by modern humans in the Old and New Worlds, because it is evident that Gran Dolina is not Olsen–Chubbuck. Above all, the technological implements (hunting weapons) available in the tool kit of the hominins of the Sierra de Atapuerca were certainly less efficient than modern hunting tools. However, several European Middle Paleolithic sites suggest the development of techniques and teamwork skills for communal hunting or at least the development of specialized hunting tactics and techniques linked to mass predation events (Jaubert et al., 2005; Gaudzinski, 2006; Rendu et al., 2009, 2012). There are several features shared by these sites that allow for the archeological recognition of communal hunting. All are large accumulations involving thousands of remains and represent at least several dozen individuals of the same species. In addition, all of the assemblages are largely dominated by a single type of prey, often monospecific in ecological terms. At each of the sites, human-caused mortality is demonstrated by several lines of evidence, such as the association of lithics and bones, the extensive green breakage, the scarcity of complete bones (specifically high marrow yielding ones), few or no anatomical connections, and an abundance of butchering marks in relation to primary access to the carcasses. All of these assemblages represent well-defined, stratified, and relatively quickly buried deposits, although in many cases, the assemblages are cumulative superimposed palimpsests of several kill episodes. In each, evidence of single mortality events can be detected, including seasonal mortality, death synchronicity, population structures of extant species, and sex/age distribution comparable with present-day herds. Finally, all of these assemblages are located in sites associated with kill facilities, often with topographic advantages. These traits fit with the four families of evidence proposed by Lubinski (2013) to infer the mass procurement of ungulates in zooarcheology: threshold bone count, human-caused mortality, single depositional episodes, and single mortality events. All of these characteristics are fulfilled in the case of the Gran Dolina TD10.2 bison bone bed.

The early development of tactical hunting strategies and techniques such as communal hunting suggested by our work is very
significant in terms of social implications. There is a consensus that hunting is the most skill- and strength-intensive foraging activity. This is based on the fact that hunting return rates peak later in life than most other food acquisition activities (Walker et al., 2002). The combination of skills, wisdom, and experience necessary for the successful development of hunting, regardless of type, is associated with a slow social learning process and the transmission of knowledge among group members (Walker et al., 2002; Hewlett et al., 2011). In the case of communal hunting, ethnographic information indicates that these practices are surrounded by symbolic elements, often related to the generational transmission of how, when, and where to perform the mass killings.

6. Conclusions

The zooarcheological analysis of the faunal assemblage of the Gran Dolina TD10.2 bison bone bed presented here shows that the cave was used as the kill-butchering site for several seasonal events of mass communal hunting in which herds of bison were slaughtered and exploited intensively by the hominins that occupied the cave. The main contribution of this research is the convincing demonstration that humans at Atapuerca were communally driving and killing bison at least 400,000 years ago. Similarly, the early existence of mass communal hunting as a predation technique informs us regarding the emergence of cognitive, technological, and social skills assumed to have emerged only recently. The active cooperation of many individuals in a previously conceived plan, not only for the hunt, but also for processing, transporting, and meat sharing, was possible only with a wide knowledge of the seasonal cycles of prey, high anticipatory capacity, high social integration, and cohesion similar to that exhibited by other modern communal hunters. Communal hunting of large, dangerous prey has long been held up by archeologists as one of the clear hallmarks of modern human behavior, proof of our ability to cooperate in large social groups, proof of long-term planning ability, and proof of sophisticated weaponry and hunting strategies. Our work pushes the emergence of these capacities much further back in time, suggesting deep roots for some cognitive and social skills that have been previously linked with modern humans.

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Supplementary Online Material

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