The role of small prey in human subsistence strategies from Early Upper Palaeolithic sites in Iberia: the rabbits from the Evolved Aurignacian level of Arbreda Cave

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Abstract

In the western Mediterranean changes in hunter-gatherer subsistence strategies have been identified from the Early Upper Palaeolithic. These changes are characterised by broadening of diet and intensification of small prey exploitation. In the case of the Iberian Peninsula region, intensified small prey exploitation is evidenced by the hunting of large quantities of European rabbit (*Oryctolagus cuniculus*), which are usually a ubiquitous feature of faunal assemblages from archaeological sites. Before interpretations of the significance of such assemblages can proceed, however, it is necessary to confirm their anthropic origin, since a wide range of predators are agents of accumulation. The taphonomic signatures observed for predators are here applied to the analysis of leporid remains from the Evolved Aurignacian layer of Arbreda Cave (North-East Iberia). The aims of this work are twofold: (1) to identify the agent/s of accumulation; and (2) to assess possible changes in small prey use during the Middle to Upper Palaeolithic transition. Our results suggest that rabbit assemblages were most likely hunted and consumed by humans and that rabbits became a primary resource in hunter-gatherer diet from the Early Upper Palaeolithic.

Keywords

1. Introduction

The Aurignacian is an Early Upper Palaeolithic cultural technocomplex that is traditionally associated with the movement of anatomically modern humans (AMH) into Europe and the subsequent replacement of Neanderthal populations. The Aurignacian is marked by a variety of cultural innovations including: the systematic production of tools and other artifact types using organic materials such as bone, antler, and ivory; personal body adornment; and artistic expressions in the form of mobiliary and parietal artwork (e.g. Knecht, 1993; Liolios, 2006; Teyssandier *et al.*, 2010; Vanhaeren and d'Errico, 2006). The Aurignacian technocomplex comprises a succession of culturally distinct phases, which are chronologically and techno-typologically different (Banks *et al.*, 2013; Mellars, 2006). In the Iberian Peninsula, the last of these phases, the Evolved Aurignacian (31-28 Ka), is found in the Cantabrian region, Mediterranean Spain and central Portugal (Zilhão, 2006).

In the western Mediterranean changes in hunter-gatherers subsistence strategies have been identified during the Early Upper Palaeolithic. These changes are characterised by broadening of the diet and intensified small prey exploitation (Aura *et al.*, 2002, 2009; Hockett and Haws, 2002; Jones, 2006; Pérez Ripoll, 2001; Stiner and Munro, 2002; Villaverde *et al.*, 1996). In the Iberian Peninsula, intensified small prey exploitation is mainly evidenced through the hunting of large quantities of European rabbit (*Oryctolagus cuniculus*), which are usually the most abundant taxa among faunal remains in archaeological sites from this period (Fa *et al.*, 2013). Although several studies have demonstrated that rabbit exploitation can be found in even the older archaeological sites (Cochard *et al.*, 2012; Sanchis Serra and Fernández Peris, 2008), their consumption seems to intensify from the Upper Palaeolithic, coinciding with the arrival of AMH (Aura *et al.*, 2002).

In light of the suite of cultural innovations during this period, information on the subsistence behaviors of Aurignacian groups is of considerable relevance, since it can

inform upon technology, communication and mobility. However, the acquisition and consumption of small prey during the Aurignacian is still poorly understood. Zooarchaeological studies from this region and period are scarce and there are no taphonomic studies which critically assess assemblage formation processes.

The origin of archaeological rabbit remains is a key issue underlying this debate, as rabbits are an important source of food for a large number of non-human predators (Delibes and Hiraldo, 1981). Terrestrial carnivores and raptors are regular visitors to caves and rock-shelters where prey leftovers and pellets or scats may accumulate. In addition, rabbit accumulations could be intrusive as a result of natural death in their burrows. In fact, taphonomic studies of archaeological assemblages have shown that they are often the product of combinations of anthropogenic and/or not anthropogenic agents (Hockett and Haws, 2002; Lloveras *et al.*, 2010, 2011; Pérez Ripoll, 2004; Rodríguez-Hidalgo *et al.*, 2013a; Sanchis Serra and Fernández Peris, 2008). Therefore, in order to understand human subsistence activities in the past it is essential to establish how a given faunal assemblage accumulated. In recent years, systematic actualistic studies on modern leporid (rabbits and hares) remains originating from natural populations, terrestrial carnivores, raptors and humans have been conducted to identify the corresponding taphonomic signatures (Cochard, 2004; Lloveras *et al.*, 2008a, 2008b, 2009a, 2009b, 2012a, 2012b, 2014a, 2014b; Rodríguez-Hidalgo *et al.*, 2013b; Sanchis, 2000; Sanchis *et al.*, 2011; Sanchis Serra *et al.*, 2014; among others). The value of these datasets in developing refined understandings of archaeological accumulations of leporids has already been emphasized (Lloveras *et al.*, 2010, 2011). In the present work the patterns described in actualistic studies are applied to the rabbit and hare remains assemblage recovered in the Evolved Aurignacian level from Arbreda Cave, a site located at Serinyà (Girona, Spain) on the Northeast of the Iberian Peninsula (Fig. 1). The aims of this work are twofold: (1) to identify the agent/s responsible for the accumulation; and (2), to assess possible changes in small prey use during Middle to Upper Palaeolithic transition. The approach followed here

provides an opportunity to afford new insight into the subsistence behavior of early modern human groups during the Evolved Aurignacian and to establish when rabbits became a predominant dietary resource.

2. Archaeological context

The Arbreda Cave forms part of the Reclau cave system (Serinyà, Catalonia, Spain), a clustered formation perched on a small talus of a somewhat karstic cascading travertine, above the Serinyadell Stream (Fig. 1). These shelters look out towards the west at a height of about 200 m a.s.l. The archaeological site is one of the richest and most significant Palaeolithic deposits in northeast Iberia, preserving one of the longest continuous stratigraphic and cultural sequences in the area. Currently, it provides the most detailed information about the changes that occurred between late Middle and early Upper Palaeolithic in the Eastern Pyrenees (Maroto *et al.*, 1996). The over 7 m-thick exposed stratigraphic sequence spans from Mousterian, Archaic Aurignacian, Evolved Aurignacian to Gravetian and Solutrean levels (Maroto *et al.*, 1996; Soler and Maroto, 1987) (Fig. 2).

The Evolved Aurignacian level (level G) presents a minimum average thickness of 40 cm dated to 30,950 ± 220 BP (Maroto *et al.*, 2012). This level is the richest in lithic industry (N retouched= 682) from the Arbreda Cave sequence, cut essentially in flint and quartz (61% and 31% respectively). Tools include nosed and carinated endscrapers, burins, Aurignacian retouched blades, Dufour bladelets and points. Dufour bladelets, mostly microliths, are the most abundant. Among the quartz and quartzite tools are abundant flakes and some sidescrapers. Bone tools include a few awls and two typical split-base bone points (Sacchi *et al*., 1996; Soler and Maroto, 1987). This level also presented two interesting combustion structures made with sandstone slabs (Soler and Maroto, 1987).

Almost 18000 animal bone fragments were recovered from this level, the majority of which were rabbits (*Oryctolagus cuniculus*) (Table 1), constituting more than 98% of NISP of large and medium-sized mammals (Casellas and Maroto, 1986; Soler and Maroto, 1987). Among the ungulate remains, horses (*Equus ferus*), red deer (*Cervus elaphus*) and large bovids (cf. *Bos primigenius*) stand out. Spanish ibex (*Capra pyrenaica*) and roe deer (*Capreolus capreolus*) were also present infrequently. Carnivores were mostly represented by red fox (*Vulpes vulpes*) and wolf (*Canis lupus*) but one bear bone (*Ursus* sp) was also recovered. Hedgehog (*Erinaceus europaeus*) and hare (*Lepus* sp.) remains were also identified (Table 1). Bird remains were relatively abundant with 254 specimens identified belonging at least to 38 species (Garcia Petit, 1995). 50 fish bone fragments representing at least six different species were also identified (Muñoz and Casadevall, 1997).

3. Material and Methods

The analysed sample of leporid remains derive from the site's Evolved Aurignacian (level G) deposits (Fig. 2), specifically from squares B3, C3 and D3 (Fig. 3).

The cave's deposits were entirely wet-sieved through a 1 mm mesh.

The Number of Identified Specimens Present (NISP), Minimum Number of Elements (MNE) and Minimum Number of Individuals (MNI) were calculated as well as relative frequencies.

Age at death was estimated taking into account the epiphyseal fusion state of long bones, metapodials, scapulae and innominates (Rogers, 1982; Taylor, 1959). Only two age categories were considered: adult and immature.

Differential conservation in relation to bone density was evaluated using the bivariate *Spearman's rho* correlation (Grayson, 1984), taking into account the data provided by Pavao and Stahl's (1999) independent measures of rabbit bone density.

The analytical methodology used in the study follows the criteria applied in previous works carried out on modern leporid assemblages accumulated by different predators (Lloveras *et al.*, 2008a, 2008b, 2009a, 2009b, 2012a, 2012b, 2014a, 2014b). For the sake of clarity, the variables considered in each of the analytical parameters studied are presented below:

3.1 Anatomical representation

Relative abundance for every skeleton element was calculated (Dodson and Wexlar, 1979). In addition, proportions of skeletal elements were evaluated using the indices proposed by Andrews (1990) since they proved to be very useful when comparing anatomical representation profiles from faunal remains potentially accumulated by different predators. They are as follows:

(a) PCRT/CR – the total number of postcranial elements (limb elements, vertebrae and ribs) compared with the total number of cranial elements (mandibles, maxillae and teeth).

(b) PCRAP/CR – the total number of limb elements (long bones, scapulae, innominates, patellae, metapodials, carpals, tarsals and phalanges) compared with the total number of cranial elements (mandibles, maxillae and teeth).

(c) PCRLB/CR – the total number of postcranial long bones (humeri, radii, ulnae, femora and tibiae) compared with the total number of cranial elements (mandibles and maxillae).

Loss of distal limb elements was examined by two indices:

(d) AUT/ZE – autopodia (metapodials, carpals, tarsals and phalanges) compared with zygopodia and stylopodia (tibiae, radii, ulnae, humeri, femora and patellae);

(e) Z/E - zygopodia (tibiae, radii and ulnae) compared with stylopodia (femora and humeri).

A further index compared anterior to posterior limb elements:

(f) AN/PO – scapulae, humeri, radii, ulnae and metacarpals compared with innominates, femora, tibiae and metatarsals.

3.2 Breakage

Breakage patterns were described by the maximum length of all the identified skeletal elements. The mean value and percentages of remains less than 1mm were calculated. Percentages of complete elements, isolated teeth and articulated elements were also estimated. For immature individuals, diaphyses of long bones with unfused epiphyses were considered as complete elements. Unfused proximal or distal epiphyses were classified as fragments of long bones. Long bones cylinders (fragments of long bones with snapped ends as a result of consumption) were also recorded. Long bones fragments were analyzed while attempting to distinguish green from dry fractures (Johnson, 1985; Villa and Mahieu, 1991).

Bone fragments were categorised depending on bone type:

- patellae, carpals, tarsals and ribs were classified as complete (C) or fragmented (F);

- phalanges were recorded as complete (C), proximal (P) or distal (D) fragments. When the distinction between proximal or distal was not possible, they were recorded as fragment (F);

- vertebrae were registered as complete (C), vertebral body (VB), vertebral epiphysis (VE) or spinous process (SP);

- breakage of teeth was calculated separately for isolated and *in situ* elements (Fernández-Jalvo and Andrews 1992) and they were classified as complete (C) or fragmented (F);

- breakage categories for long bones, metapodials, mandibles, crania, scapulae and innominates follow those proposed by Lloveras *et al.* (2008a) and applied in subsequent studies (i.e. Lloveras *et al.*, 2008b, 2009a, 2012a, 2014a).

3.3. Bone surface damage

Damage to the bone surface was examined macro- and micro-scopically. Each fragment was observed under light microscope (x10 to x40 magnification).

- Based on the methodology used for micromammals by Andrews (1990) and Fernández-Jalvo and Andrews (1992), different categories of digestion damage were applied to bones and teeth separately (digestion damage categories are fully described in Lloveras et al., 2008a). Five degrees of digestion were distinguished: null (0), light (1), moderate (2), heavy (3) and extreme (4).

- Tooth/beak marks caused by predators were also identified and registered. Tooth/beak marks were classified as: tooth punctures (TPU), tooth pits (TPI), notches (NO), scoring (SCO), and crenulated / fractured edges (CRE) (Haynes, 1980, Binford, 1981). Data provided by other studies dealing with tooth/beak marks on small prey were also taken into account (Landt, 2007; Lloveras et al., 2008a, 2008b, 2009a, 2009b, 2012a, 2012b; Rodríguez-Hidalgo et al., 2013b; Sanchis Serra et al., 2011).

- Cut marks were classified following the same methodology used in Lloveras et al. (2009b). They were tallied according to element type and section of the bone and classified as longitudinal, transversal or oblique depending on their orientation to the axis of the skeletal element on which they occurred.

- Burnt bones were identified by visual examination; colour of burning damage was recorded (Shipman et al., 1984; Stiner et al., 1995) and described as light (yellow-light brown), moderate (brown) or strong (black). Burnt areas were recorded on each skeletal element, according to portion (e.g., distal, proximal) and side.

4. Results

In general, the bones are well preserved, with only a few specimens exhibiting calcareous encrustation that in some cases obscured the observation of taphonomic traits. The number of leporid bones and teeth identified to skeletal element was 2953;

most were rabbits (99.9%), with only four specimens identified as hare (*Lepus* sp.).

Based on incisors counts, the estimated minimum number of individuals (MNI) is 43.

Age at death revealed a clear preponderance of adult individuals, which accounted for 82.1% of the sample.

According to Pavao and Stahl's (1999) criteria, there was no statistically significant correlation between the frequency of rabbit skeletal portions and their density (rho=0.322, p=0.224). This indicates that the preservation of rabbit remains within the Evolved Aurignacian level of Arbreda Cave was generally unaffected by density mediated attrition.

4.1 Anatomical representation

Table 2 shows the anatomical composition of the identified remains. The entire skeleton is represented – teeth, proximal and medial phalanges, and cranial remains were the most frequent elements (N%); the smallest elements, carpal/tarsal, distal phalanges and patellae were the scarcest. This is probably explained by recovery loss as these elements are very small and are frequently overlooked during excavation. The relative abundance of skeletal elements (RA%) is also shown in Table 2 and Fig. 4. The mean value (44.7%) is low indicating an important loss of bones in the assemblage. The best-represented elements were the incisors (98.3%), ulnae (86%) and mandibles (83.7%), whilst carpals/tarsals, ribs and distal phalanges were rare (2%, 2.4% and 3.2% respectively).

Relative proportions of skeletal elements are shown in Table 3. Results indicate that:

- there is a deficiency in the numbers of postcranial compared to cranial remains; however, when cranial elements are compared to long bones (PCRLB/CR), the sample shows equilibrium in both types of element (96.7), indicating a good representation of long bones;

- comparisons of lower to upper limb elements (AUT/ZE) shows an important loss of the former; however, as the Z/E index shows equilibrium between zygopodia and

stylopodia (94.3), the deficit affects only the autopodia (particularly the smallest ones, i.e., distal phalanges and carpals/tarsals);

- the AN/PO index reveals a slight deficiency in the number of posterior limb elements compared to anterior limb elements.

4.2. Breakage

The size of leporid bone fragments ranges between 1.5 and 159 mm; the average maximum length was 14.3 mm and 64% of the rabbit remains had length values over 10 mm. The percentage of complete elements was 32.2%. Values vary according to bone size, with the highest percentages obtained for the smallest bones: carpals/tarsals; patellae; phalanges; teeth and astragali (Fig. 5, Table 4). Long bones were complete in only 0.4% of cases. A total of 287 (30%) teeth were recovered *in situ.* Breakage categories (Table 4) show that:

- crania were never complete and their fragments were mostly identified by parts of the neurocranium (NC) and maxilla (M);

- mandibles were complete in only 0.7% of cases and their fragments were mainly represented by body portions (including MB and MBB);

- teeth located *in situ* were complete in 91.1% of cases but isolated teeth were complete in only 45.5% of cases;

- vertebrae were complete in 20.4% of cases, their fragments were mainly represented by the vertebral body (VB), there were a few instances of spinous processes (SP) and vertebral epiphyses (VE);

- innominates were complete in only 1% of cases, most fragments were represented by portions containing the acetabulum (AISIL, AIL, AIS), illium and ischium fragments (IL, IS) were also common;

- scapulae were complete in only 1.3% of cases and most fragments comprised the glenoid cavity (GC, GCN, GCNF);

- all breakage categories were found on the limb bones; only one ulna, one femur and one tibia are complete; fragments of diaphysis were the most common; fragments comprising the proximal epiphysis were the more abundant for radius, ulna and femur, whilst most humerus and tibial fragments included distal epiphyses;

- metacarpals and metatarsals were more complete than long bones (48.8% and 10.2% of cases respectively);

- astragali were more frequently complete (66.7%) than calcanea (42.9%);
- 75.1% of phalanges were complete.

The study of long bones fragments revealed a large number of shaft fragments (39.8% of the total number of long bone remains). The number of cylinders of humeri (N=20), femora (N=21) and tibiae (N=21) was also high, representing 13.2% of all remains of these elements combined (Fig. 6). Most long bone fractures (86.9%) were attributed to fresh breakage, presenting curved shaped fractures, oblique angles and smooth edges (Fig. 7).

4.3. Bone surface damage

Digestion damage was evident in only 4.8% of the leporid sample (Table 5, Fig. 7). Most remains showed a moderate and heavy degree of digestion damage; specifically, 0.5% of the skeletal elements were altered by a light degree, 1.6% by a moderate degree, 1.6% by a heavy degree and 0.03% by an extreme degree of corrosion. Bones and teeth were altered in similar proportions (Fig. 8). Among bones, patellae, astragali and calcanea were slightly more damaged.

Tooth/beak marks were observed on 50 bones (1.7% of the sample). The most common form of damage was tooth pits (40.9%) and tooth punctures (30.3%), followed by fractured/crenulated edges (18.2%), scoring (7.6%) and notches (3%) (Fig. 7). Pits and punctures occurred on humeri (6), femorae (5), radii (4), ulnae (4) innominates (4), scapulae (3), tibiae (3), vertebrae (3), calcanea (3), metatarsii (2), phalanges (2), mandibles (1), astragali (1), ribs (1) and teeth (1). On long bones they were mostly situated close to the proximal and distal ends (77.3%) and along the shaft (21.7%); on the innominate under the acetabulum (50%) and on the illium surface (50%); and in the scapula around the glenoid cavity (100%). In some cases (7) the same bone displayed several punctures.

Tooth marks were caused by carnivores in at least three cases, evidenced by the presence of gnawing damage, multiple punctures and pits in the same specimen, and the location of marks (on different sides of the same bone). However, given the low frequency of tooth-marked elements, the high percentage of pits (shallow depressions), and their location on the bones, it remains possible that most of the marks observed in the present study were inflicted by human teeth (Landt, 2007; Lloveras *et al.*, 2009b; Saladié et al., 2013; Sanchis Serra *et al.*, 2011). Tooth pits on long bones, at least in 10 cases could be related to fragmentation of epiphysis for marrow consumption. Furthermore, in three cases the same bone displayed tooth pits and cut marks.

A total of 19 bones (1% of bones) displayed cut marks (Fig. 7). They were mostly observed on long bones (12 cases), calcanea (2), metapodia (1), mandibles (1), astragalii (1), innominates (1) and vertebrae (1). On long bones, cut marks were situated on shafts (72.7%) and close to the epiphyses (27.3%). Most cut marks were transverse to the principal axis of the bone. In long bone diaphyses, such transverse marks co-occurred with oblique marks. Cut marks on mandibles, metapodials and

innominates may occur during skinning and disarticulation of rabbit carcasses whereas those on long bone shafts probably relate to defleshing (Lloveras *et al*., 2009b).

Burning damage was observed on 6.5% of the studied remains. In general, burning was not located on any particular part of the skeletal elements but in 10% of cases, it was concentrated on the terminal parts. Different kinds of bones were affected with a predominantly strong and moderate intensity, but astragali (30.8%), calcanea (19.6%), scapulae (15.6%) and limb bones (9%) were more affected than other skeletal remains.

5. Discussion

The large numbers of rabbit remains recovered from Evolved Aurignacian levels at Arbreda Cave were found associated with animal bones from a range of taxa. Since both human and non-human predators could accumulate this type of assemblage, the extent to which it is anthropogenic in origin demands assessment.

5.1. Comparisons with other rabbit assemblages

The anthropic pattern of leporid exploitation is characterized by a procurement strategy focused on adults, which usually constitute more than 80% of hunted individuals (Brugal, 2006; Cochard, 2004b; Guennouni, 2001; Hocket, 1991; Hocket and Ferreira Bicho, 2000; Rillardon and Brugal, 2014), although lower percentages (around 50-60%) have also been noted (Martínez-Valle, 1996; Sanchís Serra & Fernández Peris, 2008), especially when rabbits are mass collected in warrens (Jones, 2006). The frequency of adult individuals from level G of Arbreda Cave is placed within that range (82.1%). Further, comparisons with non-human predators show that the frequency of adult individuals in Arbreda is higher than in any of the modern samples, with the exception of one red fox (*Vulpes vulpes*) scat accumulation (Table 6). However, large variability has been observed in the age profiles of leporid assemblages accumulated

by most predators, depending on factors such as the availability of prey or the seasonality of the hunt. As an example, the percentage of adult rabbits in Eagle Owl (*Bubo bubo*) accumulations may vary between 10% and 80% (Cochard, 2004b; Guennouni, 2001; Guillem and Martínez-Valle, 1991; Lloveras *et al.*, 2012b; Sanchis, 2000). Therefore, the age profile of the Evolved Aurignacian leporids from Arbreda Cave fits with an anthropic accumulation pattern, but the intervention of non-human predators cannot be excluded.

Anthropic accumulations are also characterised by the presence of all skeletal elements, indicating the transport of whole carcasses to the site. In the Arbreda sample, despite the scarcity of the very small elements (which may reflect differential recovery)

anatomical part representation indicates whole skeletons were present; no differential transportation of any part of the rabbit carcasses is evident, which may occur with some predators, e.g. some raptors usually cut and eat the head of the rabbit before bringing it to the nest (Donazar,1988).

Although there is considerable variability in the anatomical profile of anthropogenic assemblages, mandibles, long bones, scapulae and innominates are typically the best represented remains (Brugal, 2006; Cochard, 2004b; Guennouni, 2001; Hockett, 1991; Hockett and Haws, 2002). The relative abundance profile for the Evolved Aurignacian from Arbreda Cave reveals that teeth, mandibles and long bones were the best represented elements; scapulae and innominates were also well represented. This is close to the anatomical profile expected for anthropogenic accumulations. Added support is provided by the contrasting anatomical representation pattern for non-human predators (Table 6). Lynx scats provide the most similar profile with an abundance of cranial remains and forelimbs outnumbering hindlimb bones (Lloveras *et al.*, 2008a).

In anthropic accumulations, long bone breakage resulting from bone marrow processing (normally by dental breakage) generates an assemblage containing multiple fragments of epiphysis and more than 5% of long bone cylinders (see Table 7)

when all of these elements are combined (Cochard, 2004b; Hockett, 1991, 1995, 2006; Pérez Ripoll, 2004, 2005). In the Evolved Aurignacian level at Arbreda Cave, the high proportion of femorae, tibiae and humeri cylinders (13.3%), as well as the abundance of epiphysis fragments (33.7%) points to the extraction of marrow from long bones. The percentage of complete bones (32.2%) and complete long bones (0.4%) is much lower in the Arbreda sample compared with actualistic studies of other predators with two exceptions, Spanish Imperial Eagle (*Aquila adalberti*) pellets and carnivore (red fox and Iberian lynx (*Lynx pardinus*)) scats. However, these accumulations are characterised by very high percentages of digested remains (98%-99.5%). The low numbers of skeletal elements affected by digestion corrosion in level G at Arbreda Cave (4.8%), excludes these agents of accumulation.

Recovery of meat on fresh carcasses for human consumption is characterized by the presence of cut marks and burnt bones, particularly the distal ends of long bones (Lloveras *et al*., 2009b). In the Evolved Aurignacian Arbreda sample, 1% of bones display cut marks and 6.5% exhibit burning damage. Both percentages fit within the range observed for anthropogenic leporid accumulations of the Upper Palaeolithic of the Mediterranean (Table 7).

Traditionally, tooth marks have been attributed to non-human predators. However, ethnoarchaeological as well as experimental work has shown that humans can make many modifications during chewing (Landt, 2007; Lloveras *et al*., 2009b; Saladié *et al*., 2012; Sanchis Serra *et al*., 2011). The main problem is that it is not a straightforward matter to distinguish tooth marks caused by humans and other predators. The most common damage caused by human teeth relates to the removal of minimal to moderate amounts of cancellous bone tissue (e.g., removal of trochanters or ends of ribs) (Landt, 2007) and to bone breakage for marrow consumption (Sanchis Serra *et al*., 2011). Punctures are rare, mainly located on flat bones and long bone diaphyses, and damage is less severe than gnawing produced by carnivores (often multiple damage in the form of pits, punctures, scores, furrows, etc. in the same bone).

Following these criteria, at least 23% of tooth marks registered on leporid bones from the Evolved Aurignacian assemblage from Arbreda, appear to have been caused by human feeding activities.

In summary, the taphonomic pattern established for leporid remains from Evolved Aurignacian Arbreda assemblage is clearly anthropogenic. The presence of a small number of digested remains and carnivore-gnawed bones indicates that other predators, such as small terrestrial carnivores (probably red fox), may have made marginal contributions to the accumulation.

5.2. Middle to Upper Palaeolithic transition at Arbreda Cave

A previous taphonomic study of the leporid assemblage from the Mousterian level at Arbreda Cave showed that small terrestrial carnivores were responsible for the accumulations (Lloveras *et al*., 2010) and it was concluded that the contribution of rabbits and hares to the subsistence pattern of hunter-gatherers from this period must have been occasional. Results obtained in the present study differ clearly in all variables analysed (Table 8). Relative abundance profiles show higher values for cranial remains, mandibles, scapulae and forelimb bones in the Aurignacian sample. Moreover, the percentages of complete bones indicate that the leporid remains were more fragmented (32.2% vs 43.4%). With regard to long bone breakage, data show that the number of long bone cylinders is clearly higher in the present study (13.3% vs 3.2%). On the contrary, the presence of digestion damaged remains is much higher in the Mousterian (32.4% vs 4.8%) as well as the number of carnivore tooth marked bones (2.5% vs 1.3%). Furthermore, there are no cut marks in the Mousterian sample and the presence of burning damage is minimal (0.5%).

All the data converge upon the conclusion that by the Upper Paleolithic, subsistence strategies of human groups at Arbreda Cave had changed. Certainly by the Evolved Aurignacian small prey, especially rabbits, were an important dietary resource.

Changes in the frequencies of other animal species are also evident. In the Mousterian, the abundance of large carnivores, i.e. cave bear, demonstrated that the cave functioned as a carnivore den, being occupied by humans only intermittently (Maroto *et al*., 1996; Lloveras *et al.,* 2010). In contrast, by the Evolved Aurignacian the scarcity of carnivores in the assemblage indicates that they no longer played a significant role in accumulating bone within the cave. In fact, the evidence collected suggests that the site functioned as a recurrently occupied human settlement.

The centrality of rabbits in the diet of Upper Palaeolithic hunters-gatherers from western Mediterranean Europe, particularly in the Mediterranean bioclimatic zone of the Iberian Peninsula, has been debated extensively. Results similar to those obtained in the present study have been generated at several sites from Portugal (Cochard and Brugal, 2004; Hockett and Ferreira Bicho, 2000; Lloveras *et al*., 2011; Manne and Bicho, 2009) and Spain (Ibañez and Saladié, 2004; Pérez Ripoll, 2004) in Gravettian, Solutrean and Magdalenian levels; and in the South of France (Cochard, 2004b; Cochard and Brugal, 2004; Jones, 2012; Rillardon and Brugal, 2014) from the Magdalenian (see Table 7). Nevertheless, an overview of faunal remains recovered from Early Upper Palaeolithic levels from western Europe highlights the geographic diversity of subsistence strategies. In Spanish Cantabria, hunting mostly focuses on ibex (*Capra ibex*) and red deer (*Cervus elaphus*) (Pike-Tay *et al*., 1999) whilst in most of northern European areas horses (*Equus ferus*) and reindeer (*Rangifer tarandus*) are the most common prey (Grayson and Delpech, 2002; Niven, 2007). In brief, these results make clear the capacity of Early Upper Palaeolithic hunter-gatherers to adapt their strategies to the resources present in each region. The ultimate cause for the adoption of different strategies is likely to reside in factors related to the availability of the different prey species and to human demography, with corresponding implications where caves and rock-shelters are concerned, for patterns of site function and site use that also witnessed significant change over time.

This adapatibilty, may also be evidenced at some Middle Palaeolithic sites in southern Europe. For example, Morin (2014) has argued that changes in large prey exploitation in the faunal assemblages from late Middle Palaeolithic and Early Upper Palaeolithic southwestern France were stimulated by changes in climate. Evidence at other Mousterian sites indicates the exploitation of small prey such as birds or tortoises (Blaco and Fernández Peris, 2012; Blasco et al., 2014; Morin and Laroulandie, 2012; Peresani et al., 2011) and rabbits (Guennouni, 2001; Martínez Valle, 1996; Rufà et al., 2014; Sanchis Serra and Fernández Peris, 2008). Such evidence has been used to question the argument that broadened diet and dietary intensification occurred exclusively in the Middle to Upper Palaeolithic transition (Aura *et al.*, 2002, 2009; Hockett and Haws, 2002; Stiner et al., 2000; Stiner and Munro, 2002). However, while the expoitation of small prey certainly occurred during the Middle Paleolithic, they still only formed a relatively small component of diet. More data on Early Upper Palaeolithic faunal assamblages is essential in order to inform this debate concerning the intensification of small prey hunting.

6. Conclusion

In this study it has been shown that in Arbreda Cave, rabbits become a primary prey for humans from at least the Evolved Aurignacian period. Distinguishing leporid bones accumulated by humans and other kind of predators is imperative to accurately understand human subsistence activities in the past, especially in the Iberian Peninsula and the Mediterranean region where these taxa are abundant. In recent years, several actualistic studies with modern leporid remains have been conducted to identify differences in the taphonomic signatures produced by competing predators using a standardised methodology, permitting comparison of the same variables in archaeological samples. Our results show that at Arbreda Cave during the Evolved Aurignacian, humans were the primary agent of rabbit accumulation whilst raptors were

excluded and small carnivores made a minimal contribution. Taphonomic and zooarchaeological data reveal that during this period the cave was mostly a human settlement with short periods of abandonment, in which mainly small carnivores probably used the site as a den. This is a totally different pattern to that recognized during the Mousterian. More studies of this kind are needed to establish if this pattern recurs throughout Mediterranean southwestern Europe and to understand in greater detail why and when changes in the diet of Upper Palaeolithic humans groups occurred.

Acknowledgements

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List of Tables

Table 1. Numbers (NISP), percentages (%NISP) and minimum number of individuals (MNI) of faunal remains in the Evolved Aurignacian Level of Arbreda Cave. *Numbers of hare and rabbit remains are approximate.

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Table 3. Proportions of different parts of the skeleton in Evolved Aurignacian sample from Arbreda Cave.

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incisive part (IP), mandible body + incisive part (MBI), mandible body (MB), mandible body + branch (MBB) and condylary process (CP). **Crania** as: complete (C), incisive bone (IB), incisive bone + maxilla (IBM), maxilla (M), zygomatic arch (ZA) and neurocranium (NC). **Innominates** as: complete (C), acetabulum (A), acetabulum + ischium (AIS), acetabulum + ischium + illium (AISIL), acetabulum + illium (AIL), ischium (IS) and illium (IL). **Scapulae** as: complete (C), glenoid cavity (GC), glenoid cavity + neck (GCN), glenoid cavity + neck + fossa (GCNF), neck + fossa (NF) and fossa (F). **Vertebrae** as: complete (C), vertebral body (VB), vertebral epiphysis (VE) and spinous process (SP). **Phalanges** as: complete (C), proximal fragment, (P), distal fragment (D) and fragment (F). **Patellae, carpals/tarsals, calcanea, astragali, ribs and teeth** as: complete (C) and fragment (F).

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marks on rabbit axis. (J, K, L): cut marks on metatarsal, proximal epiphysis of femur and a burnt diaphysis of femur.

Figure 8. Percentage of bone and dental remains included in each digestion category.

TABLE 1

Species	NISP	%NISP	MNI
Equus ferus	81	36.8	5
cf. *Bos primigenius*	23	10.5	3
Cervus elaphus	81	36.8	5
Capreolus capreolus	5	2.3	1
Canis lupus	6	2.7	2
Vulpes vulpes	10	4.5	1
Ursus sp	1	0.5	1
Erinaceus europaeus	13	5.9	2
TOTAL	220	100.0	20
Lepus sp*	72		
*Oryctolagus cuniculus**	17694		
Birds	250		
Fish	50		

TABLE 2

	NISP	NISP %	MNE	RA %
Cranium	206	7	25	58.1
Mandible	146	4.9	72	83.7
Incisor	229	7.8	169	98.3
Upper molar	411	13.9	383	74.2
Lower molar	317	10.7	278	64.7
Scapula	77	2.6	49	57
Humerus	117	4	62	72.1
Radius	104	3.5	54	62.8
Ulna	113	3.8	74	86
Metacarpus	82	2.8	62	14.4
Innominate	95	3.2	39	45.3
Femur	198	6.7	54	62.8
Patella	24	0.8	24	13.9
Tibia	141	4.8	36	41.9
Metatarsus	127	4.3	80	23.3
Calcaneum	56	2.1	44	51.2
Astragalus	39	1.3	36	41.9
Carpal/tarsal	21	0.7	21	2
Phalanx 1/2	216	7.3	198	13.5
Phalanx 3	25	0.8	25	3.2
Vertebra	162	5.5	132	10.2
Rib	47	1.6	25	2.4
TOTAL	2953		1942	

TABLE 3

INDICES %	
PCRT / CR	21.2
PCRAP / CR	26.0
PCRLB / CR	96.7
AUT/ZE	18.8
Z / E	94.3
AN / PO	112.0

TABLE 4

BREAKAGE CATEGORIES												

Long bones and metapodial	C		PE		PES		S		SDE		DE	
	N	%	N	%	N	%	N	%	N	%	N	%
humerus	0	0	21	17.9	5	4.3	28	23.9	35	29.9	28	23.9
radius	0	0	1	1	53	51	30	28.8	20	19.2	0	0
ulna	1	0.9	15	13.3	61	54	27	23.9	6	5.3	3	2.6
femur	1	0.5	49	24.7	13	6.6	103	52	5	2.5	27	13.6
tibia	1	0.7	9	6.4	15	10.6	80	56.8	20	14.2	16	11.3
metacarpus	40	48.8	1	1.2	21	25.6	0	0	19	23.2	1	1.2
metatarsus	13	10.2	1	0.8	66	52	1	0.8	41	32.3	5	3.9

Mandible	N	%	Cranium	N	%	Innominate	N	%	Scapula	N	%
C	1	0.7	C	0	0	C	1	1	C	1	1.3
IP	19	13	IB	30	14.6	A	7	7.3	GC	1	1.3
MBI	39	26.7	IBM	0	0	AIS	22	23.2	GCN	34	44.2
MB	69	47.3	M	64	31.1	AISIL	9	9.5	GCNF	13	16.9
MBB	5	3.4	ZA	45	21.8	AIL	22	23.2	NF	17	22.1
PC	13	8.9	NC	67	32.5	IS	11	11.6	F	11	14.3
						IL	23	24.2			

Vertebrae	N	%	Ribs	N	%	Phalanges 1/2	N	%	Phalanges 3	N	%
C	33	20.4	C	4	8.5	C	159	73.6	C	22	88
VB	100	61.7	F	43	91.5	P	40	18.5	F	3	12
VE	7	4.3				D	17	7.9			
SP	22	13.6									

Patella	N	%	Car/tar	N	%	Cal	N	%	Ast	N	%
C	24	100	C	21	100	C	24	42.9	C	26	66.7
F	0	0	F	0	0	F	32	57.1	F	13	33.3

Teeth	"in situ"						Isolated					
	Incisors		Upper molars		Lower molars		Incisors		Upper molars		Lower molars	
	N	%	N	%	N	%	N	%	N	%	N	%
C	29	67.4	76	100	168	100	36	19.4	201	60	68	45.6
F	14	32.6	0	0	0	0	150	80.6	134	40	81	54.4

TABLE 5

	DIGESTION DAMAGE									
	Null		Light		Moderate		Heavy		Extreme	
	N	%	N	%	N	%	N	%	N	%
Cranium	205	99.5	0	0	1	0.5	0	0	0	0
Mandible	144	98.6	1	0.7	1	0.7	0	0	0	0
Incisor	219	95.6	1	0.4	5	2.2	4	1.7	0	0
Upper molar	393	95.9	0	0	5	1.2	12	2.9	0	0
Lower molar	307	96.8	2	0.6	3	0.9	5	1.6	0	0
Scapula	71	92.2	1	1.3	3	3.9	2	2.6	0	0
Humerus	106	92.2	0	0	6	5.1	3	2.6	0	0
Radius	95	91.3	1	1	4	3.8	4	3.8	0	0
Ulna	99	88.4	0	0	7	6.2	6	5.4	0	0
Metacarpus	79	96.3	2	2.4	0	0	1	1.2	0	0
Innominate	91	95.8	1	1.1	2	2.1	1	1.1	0	0
Femur	191	96.5	1	0.5	4	2	2	1	0	0
Patella	17	70.8	0	0	4	16.7	3	12.5	0	0
Tibia	135	97.1	0	0	1	0.7	3	2.2	0	0
Metatarsus	119	93.7	2	1.6	5	3.9	1	0.8	0	0
Calcaneum	47	83.9	1	1.8	1	1.8	7	12.5	0	0
Astragalus	32	82.1	1	2.6	3	7.7	3	7.7	0	0
Carpal/tarsal	21	100	0	0	0	0	0	0	0	0
Phalanx 1/2	211	97.7	0	0	4	1.9	1	0.5	0	0
Phalanx 3	25	100	0	0	0	0	0	0	0	0
Vertebra	152	93.8	0	0	4	2.5	5	3.1	1	0.6
Rib	47	100	0	0	0	0	0	0	0	0
TOTAL	2796	95.2	14	0.5	63	1.6	63	1.6	1	0.03

LEPORID COMPARISONS	Eagle Owl *Bubo bubo*		S. Imperial Eagle *Aquila adalberti*	Bonelli's Eagle *Aquila fasciata*	Iberian lynx *Lynx pardinus*		Fox *Vulpes vulpes*		Arbreda Cave Evolved Aurignacian
Reference	Lloveras et al. 2009		Lloveras et al. 2008b	Lloveras et al. 2014b	Lloveras et al. 2008a	Rodríguez-Hidalgo et al. 2013	Lloveras et al. 2012a		Present study
Origin	Nest	Nest	Pellets	Nest	Scats	Non-ingested	Scats	Non-ingested	
NISP	1808	1932	824	438	1522	9564	265	639	2953
RA% >values	cal-inn-fem	cal-inn-tib	phal 3-u mol-tib	cra-u mol-inn	man-teeth-cra	tib-cal-mts	long bone-sc	mts-ast-tib	teeth, man, long bone
RA% <values	mtc-c/t	rad-c/t-mtc	rib-fem-rad	mtc-rib	c/t-ver-rib	sc-ver-hum	mtc-c/t-inn	cr-sc-rib	c/t, rib, phal
PCRT/CR	+postcranial	=	+cranial	+cranial	+cranial	+postcranial	=	+postcranial	+cranial
P/D	+proximal	+proximal	+distal	+proximal	+proximal	+distal	+proximal	+distal	+proximal
AN/PO	+hindlimb	+hindlimb	+hindlimb	+hindlimb	+forelimb	+hindlimb	+hindlimb	+hindlimb	=
Complete elements %									
Mean value long bones	14.6	10.8	0	51.7	2.5	37.6	0	5.4	0.4
Mean value total	53.9	45.9	27	74.7	43	73.2	12	89.4	32.2
Length (in mm)									
Minimum	2.3	2.5	1.8	1.7	1.1	3	3	4	1.5
Maximum	86.3	90	36.1	89.6	30.1	69	26.8	86.2	159
%<10 mm	49	40	73	54.9	80	19.7	61	28	36
% Digested remains	68.8	65.6	98	31.2	97.2	0	99.5	0	4.8
% Digested long bones	88.9	83.9	100	31	100	0	100	0	6.3
Degree									
Null	31.2	34.4	2	68.8	2.8	-	0	-	95.2
Light	40.2	40.2	18.2	2.3	12	-	6	-	0.5
Moderate	19.8	19.8	46.8	7.9	22	-	26	-	1,6
Heavy	8	5.3	27.4	14.4	43.8	-	43	-	1.6
Extreme	0.7	0.15	5.6	6.5	19.3	-	25	-	0.03
Teeth/beak marks	2	1.34	0.5	2.3	0.26	0.9	3	9.5	1.7
Age - % of adults	50	50	-	41.4	21.4	-	87	-	82.1

TABLE 6

Site	Reference	Cultural level	NISP	Adults %	Cylinders %	Cut marks %	Burnt %
Arbreda Cave	Present study	E. Aurignacian	2953	82.1	13.3	1	6.5
Cendres	Pérez Ripoll, 2004	Gravettian	3729	-	-	13.4	8

Molí del Salt	Ibañez and Saladié, 2004	Magdalenian	932	-	18.3	2.5	6
Champréveyres	Cochard and Brugal, 2004	Magdalenian	739	85	-	13	1.5
Faurélie II	Cochard 2004	Magdalenian	7695	95	7.5	1.6	27.4
Bois Ragot	Cochard 2004	Magdalenian	12777	94	6.2	6.2	4.1
Moulin du Roc	Jones 2012	Magdalenian	6596	-	42.7	10	19
Vale Boi	Manne and Bicho 2009	Gravettian Solutrean Magdalenian	5828	-	-	0	7
Anecrial	Cochard and Brugal, 2004	Gravetian Solutrean	1600	98.8	70	0.02	5.7
Caldeirão	Lloveras et al. 2011	Solutrean	3705	83	27	0.8	3.1
Oullins	Rillardon and Brugal 2014	Magdalenian	470	83.3	13	2	8.5
Picareiro	Hockett and Bicho 2000	Magdalenian	8981	99.4	23.6	0	2.8

TABLE 7

LEPORID COMPARISONS ARBREDA CAVE	Mousterian	Evolved Aurignacian
Reference	Lloveras et al. 2010	Present study
NISP	2407	2953
RA% >values	hum, cal, u mol	teeth, man, long bone
RA% <values	rib, c/t, ver	c/t, rib, phal
PCRT/CR	+cranial	+cranial
P/D	+proximal	+proximal
AN/PO	+hindlimb	=
Complete elements %		
Mean value long bones	2.4	0.4
Mean value total	43.4	32.2
Length		
%<10 mm	50	36
% Digested remains	32.4	4.8
% Digested long bones	46.9	6.3
Degree		
Null	67.6	95.2
Light	7	0.5
Moderate	14.8	1,6
Heavy	9.8	1.6
Extreme	0.8	0
% Teeth/beak marks		
Anthropogenic	0	0.4
Other	2.5	1.3
Age - % of adults	71.9	82.1
Cut marks %	0	1
Burnt %	0.5	6.5
Cylinders %	3.2	13.3

TABLE 8