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Dynamic of large mammalian associations in the Pleistocene of Portugal

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ABSTRACT

For the last decade, a renewal of research in the Paleolithic of Portugal with recent excavations, studies of old collections and elaborate chronological framework allow us to present a general overview about the succession of medium to large mammal communities, at least for the Middle and Upper Pleistocene in the Portuguese territory. Some taxa are reported for the first time in the fossil record, with the survival of “archaic” species until recent period within the Pleistocene. Changes in the herbivore frequencies and local large predators’ extinctions are described for the Last Glacial, thus serving to a better understanding on the relation between paleoenvironment and subsistence human activities.

KEY WORDS
Pleistocene; mammals; Paleolithic; Portugal

Paleoenvironment reconstructions are considered one of the key-issues for understanding past human behaviour and settlement patterns. Such reconstructions are provided by different field studies as ice and marine archives or continental information, and then combined into regional or more global perspectives. A fundamental point concerns the high variability of climate in space and time, which have important implications, especially in vegetation and faunal terrestrial distributions. It becomes therefore important to favour regional studies in an integrated approach for all potential terrestrial sources (e.g., palynology, anthropology, palaeontology) found in specific sedimentary contexts.

As a first contribution, the aim of this paper is to give a general overview about the large to medium-sized mammalian associations in the Pleistocene of Portugal. Taxonomic information has been compiled in a comprehensive database that can provide a framework about distribution, paleoenvironment and biogeography of mainland mammals, especially for the Last Glacial where we have a better faunal record. These elements can afford a better appreciation on the subsistence strategies for Palaeolithic hunter-gatherers with a detailed picture in herbivore resources and degree of competition among human and non-human predators. Moreover, the Portuguese data present some specificity in the mammal stocking, in term of evolutive and endemic processes, when compared with other Iberian and west European faunal associations.

NATURE AND QUALITY OF THE AVAILABLE DATA

A database for the mammalian fauna has been completed for all the Pleistocene period. The faunal information is generally dispersed in many papers and very scarce synthetic data are available to this day1. The main faunal information comes from very initial studies made by E. Harlé (1910) and subsequent works of J. Roche (1971, 1972), O. da Veiga Ferreira (1964, 1975) and G. Zbyszewski (1943, 1963), all conducted in a period of extensive archaeological excavation.

1 We will not propose a complete bibliography here due to editorial space limitations, therefore only main papers are quoted.
tions in Portugal, particularly on Upper Palaeolithic and Mesolithic sites (see Bicho, 1999 and Zilhão, 1997 for an historical background). More recently, M. T. Antunes and J. L. Cardoso have produced important palaeontological works (e.g., 1989, 1992, 1993, 1996, 2000, 2002) outlining the existence of typical species in the fossil record; however, these studies are either from isolated finds or on mixed samples, which raises some chronological problems. In recent times, with the development of taphonomic analyses and reconsideration about human involvement on bone accumulations, different scholars (S. Davis, M. J. Valente, J. Haws and J. P. Brugal, among others: see bibliography) started more accurate zooarchaeological studies from modern excavated Palaeolithic material (also including unpublished data). In this last decade, we were presented an important input of information for the Palaeolithic of Portugal with new and modern excavations that justify the present synthesis.

Due to this historical situation different kinds of problems arise, namely the type and period of investigation, with several sites having been excavated in the mid-last century or before. These sites generally have a low resolution regarding the stratigraphy and the taphonomy data, which has resulted in studies conducted on combined samples. Nonetheless, the comparison between preliminary reports or other publications and new studies can for instance bring additional elements to precise the species composition from different levels. Another problem concerns faunal identification in relation with the paucity and the degree of conservation of remains: in particular, this is the case for proboscids, large bovids and cervids. Here, we have considered all sources of information and made a criticism review in order to afford a reliable database.

The faunal information is diverse and can be expressed in term of presence-absence and, less often, with classic analytic units such number of identified specimens and minimum number of individuals. In fact we will mostly utilize the former one, using the degree of occurrence of taxa by time-period considered, in order to collect the greatest amount of information both on the species associations and on the number of sites or levels. Moreover sites will be grouped by chronological units allowing envisioning a global view of mammal associations statistically more reliable.

These data are variable and most of them are originated from archaeological contexts. The topography and geography of the sites are important points to consider; the sites are located either in karstic cavities (cave or rockshelter), generally of small size in Portugal, or at the foot of cliffs, or found in open-air deposited in fluviatile sediments. These various geological contexts have implications on the representation and preservation of the bone material as well as the thickness of the sequence with one to several fossiliferous levels. It is noticeable that limestone areas, such as Estremadura, yield most of the prehistoric sites. In addition, the geographical dimension (see Fig. 1 for a synthetic view) determine both the occurrence of sites and the type of occupation: i.e., related data on elevation and exposure, morphology of valley, nearby water or raw material sources and change in sea levels during Pleistocene time. The later point is relevant in term of land surface changes, which strongly affects our archaeological record. All these aspects have in fine to be integrated into better paleoecological reconstructions. Additionally, the nature of occupation, especially human versus carnivore, and duration and seasonally factors had a strong influence on the taxonomic composition of fossil associations. The predators tend to select their preys within a diversified herbivore biomass but they would naturally exploit the most frequent taxa available in the ecosystems. In order to avoid biases due to the prey selection we will seek to combine our data to obtain results statistically more meaningful.

We will detail the mammal associations according to the main Pleistocene periods. Overall, we found 55 Pleistocene sites with faunal remains in Portugal, including almost 75 levels. Most of the upper Pleistocene sites are archaeological sites, often multileveled, found in cave deposits. The macrofaunal accumulations (here expressed from large rodents, as the beaver, to very large mammals, such as the elephant) are often related to human activities, which have implications on species composition favouring medium to large-sized herbivores. Globally, the faunal material is never abundant: c. 52% of the sites or levels yield less than a hundred of determinable specimens, c. 39% contains between 100 and 500 remains, and very few sites have more than 500 identifiable pieces (Galeria Pesada, Foz do Enxarique, Fontainhas, Fuminha and Buraca Escura 2e). According to this variability we have chosen to consider the presence-absence and the degree of occurrence of species in our calculation.

LOWER AND MIDDLE PLEISTOCENE

There is no fossil record in Portugal for the beginning of Quaternary and real Villafranchian associations are absent, contrasting with other numerous Spanish localities. Only one open-air site, Algoz in Algarve, yielded few remains of Hippopotamus antiquus, Cervus sp. (cf. rhenanus-perolensis), Eucladoceros sp. (cf. dicranios) and Oryctolagus lacosti (Antunes et al., 1986), attributed to the end of Lower Pleistocene with a date around 1 million year.

The Middle Pleistocene sites are essentially found in terrace or travertine deposits and often concern isolated finds, dated according to stratigraphical context (Condeixa, Santa Cruz, Conimbriga, Fujaça-Pampilhosa do Bolão, Mealhada).

2 Excluding the Leporids, which can represent several thousand remains in some Upper Palaeolithic sites.
Mealhada also presents acheulean artefacts, and a U/Th date of 329 ± 70 ky is given for Condeixa. Two other sites are situated in the Almonda karst system: Nascente in the deep karst (with a U/Th date around 150 ky) and Galeria Pesada / Brecha das Lascas (or Aroeira).

The straight-tusked elephant *Elephas (Paleoloxodon) antiquus* is the most common species (*n* = 5 occurrences); they are often old finds, probably because of the large size of bone and teeth of this species. Other Middle Pleistocene species are: *Hippopotamus incognitus* (*n* = 2) and *Homotherium latidens* (*n* = 1), the sabertooth felid, as well as taxa still present during the Upper Pleistocene: *Cervus elaphus* (*n* = 2), *Bos primigenius* (*n* = 1), *Equus caballus* ssp. indet. (*n* = 2), *Capra pyrenaica* (*n* = 1). *Homotherium*, determined from one astragalus, is found in fluvial sequence of Mealhada given as “Riss” deposits (Antunes 1986); this species is present between 900-300 Ky in Western Europe and the Portuguese specimen could indicate the probable survival of the species in this territory3.

One of the most important Middle Pleistocene sites was found recently; it’s Galeria Pesada/Brecha das Lascas located in Serra da Aire near Almonda, not far from Torres Novas. A. Marks and his team (Marks et al., 2002) excavated it between 1997-2002 and its thick karstic filling (c. 3 m) has yielded rich lithic and faunal remains, with an ESR/U/Th date around 241+ 30-22 Ky (level B2). It is a multilayered sites (six main levels in Galeria Pesada) with relatively homogenous remains through the sequence. Globally fifty species are present from bats, rodents, birds, reptiles, leporids, to medium and large mammals. Thirteen species of mammals are identified, with the dominance of two cervid species, indicating an open forest and grassland under a cool climate. One the most remarkable paleontological contributions of the site concerns the identification of some new species in the Pleistocene of Portugal (Brugal, 2004a, and in prep.: archaic *Homo* (Trinkaus et al., 2003), *Macaca sylvanus* (Barbary ape), *Dama clactoniana* (Clacton deer), *Hemigratus* sp. (Thar or Asiatic mountain goat), *Ovis ammon* (wild sheep), *Canis* *gr. etruscus*mosbachensis* (archaic wolf), *Cuo priscus* (Asiatic dhole). They are associated with *Cervus elaphus* ssp., *Equus aff. mosbachensis*, *Stephanorhinus hemitoechus*, *Sus* *scrofa*, *Ursus arctos* and *Castor fiber*. Galeria Pesada constitutes the most impressive Middle Pleistocene Portuguese site with hominin activities, original lithic industry and rich original mammal associations.

**UPPER PLEISTOCENE**

The data from the first part of this period are scanty and we can note the persistence of *Elephas (Paleoloxodon) antiquus* (isolated finds) in three last “interglacial” (OIS 5 s.l.) open-air localities (Casal do Torquato, Carregado, Meirinha). Contrastingly, the period covering the second part of Upper Pleistocene is the best represented with many sites yielding faunal accumulations. They are mostly dated from the Last Glacial, OIS 4 to 2 (c. 70-10 Ky), with some of them from the very early phases of OIS 1, and are associated with late Middle to late-middle late Palaeolithic cultural (*n* = 21 sites) or naturally deposited layers (*n* = 10). These sites are essentially located at limestone region of Estremadura in Central Portugal in relatively low elevation and 74% represents cave deposits; few are in cliffs (rockshelet), in pit-falls (aligers: Goldra, Cascais, João Ramos) or in open-air (Quinta do Gaio, Santo Antão do Tojal, Foz do Enxarrique). The number of sites/levels with mammalian faunas decreases throughout the late upper Pleistocene (see Table 1). Most of the archaeological sites are multileveled either corresponding to the same cultural period (ex. Oliveira) or ranging through several techno-complexes (ex. Lapa do Picareiro, Buraca Escura).

Overall, 57 levels can be considered with reliable faunal identifications, supported by almost 70 radiometric dates, mainly conventional radiocarbon ones. The dates concern sites not older than 40/35 Ky until around 10 Ky BP. We arranged the dated sites and its levels (uncalibrated BP), plus or minus one sigma, according to the four main techno-complexes (Fig. 1): Late Mousterian (MP), Aurignacian-Gravettian (i.e. Early Upper Palaeolithic; EUP), ProtoSolutrean-Solutrean (PS + Sol) and Magdalenian (Ma) (adapted from Gamble 1986: 135-136). The few ESR and U/Th dates have been excluded of the Fig. 1 in order to keep a more coherent framework. We have also indicated the different Heinrich events (H) and Younger Dryas (YD) for this time period, which represent millennium-scale cold events (e.g., Bard, 2002). These abrupt events have clear incidence on the Iberian margin with the polar front getting to lower latitudes as northern Portugal (42° N during the last glacial maximum, like demonstrated by several occurrence of ice-rafted debris [IRD] in cores off the coast of Portugal), accompanied by drastic cooling of up to 4-5°C. Pollen, associated with foraminifer, dinoflagellate cyst or δ18O measurements, documents the impact of these short-term environmental changes on continent (Sanchez-Goni et al., 2000; Turon et al., 2003). Six Heinrich events are known during the last glacial with dates centred around 14.5 Ky (H1), 21-22 ky (H2), 27 Ky (H3), 35 Ky (H4), e.44 Ky (H5) and e.55 Ky (H6), plus the YD of shorter duration (10.5 Ky) (Grousset, 2001). Although the accuracy of the radiocarbon ages’ calibration should be questioned (Fontugne, 2004; and see d’Errico and Sanchez Goni, 2003: 771) it seems from the distribution of dated sites (taking one sigma; see Fig. 2) that the

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3 New find from the North Sea, dated to ca. 28 Ky, seems to indicate a possible late survival of this species in some parts of Europe (Reumer, et al., 2003).
different techno-complexes are more or less bracketed in between these cold stadials, with relatively continuity and short overlap (MP-EUP); a clear gap occurred between the Solutrean and Magdalenian cultures. We have then decided to pool all the different mammal associations into these four cultural periods in order to summarize all the data and better appreciate the animal community changes. We can assume that these repeated cold events have effectively affected the mammalian distributions as they did on vegetation compositions in Iberia (Sanchez Goni et al., 2002).

Land paleoenvironmental data for the Last Glacial in Portugal are extremely limited, with few and dispersed information obtained from geology, palynology and anthracology, and on faunal record (micro and macro). Different researchers have recently proposed preliminary synthesis on a regional basis (e.g., Zilhão, 1990, 1997; Bicho, 1999; Haws, 2004) and we can immediately notice that the information is far to be continuous for this period. A better chrono-climatic and palaeoenvironmental framework, at least for OIS3, has been obtained from deep-sea cores collected off the Iberian margin (d’Errico and Sanchez Goni, 2003). A first issue concerns the evidence of a cold peak identified as the Last Glacial Maximum (LGM) not only in the mountain area of northern Portugal (periglacial condition as in Serra Estrela, for instance) but also in the lower areas, such as in Caldeirão cave (basal Solutrean) in Estremadura, based on magnetic susceptibility from cave sediments (Ellwood et al., 1998). During cold and dry phases, the vegetation obtained from pollens and charcoal studies indicates the presence of steppe grasses and herbs as well as forest-parkland with coniferous (often dominating arboreal spectrum), oaks and birch, which probably expanded during interstadial conditions from some “refugium” with Mediterranean trees and shrubs (Quercus, Olea, Pistacia). These interstadial oscillations were of short duration, known as part of Dansgaard-Oeschger events (D-O), which regularly allow more or less limited forest expansion. Elevation plays a main role in the distribution of the phytoocoenose as well as in the presence of some mammal species in some sites (especially caprines). It is a complex climatic period with a succession of cold and warm fluctuations (at least about thirty for OIS3) and the mainland faunal records have a lower resolution when compared with deep-sea or ice core information. Deglaciation is also marked by several short climatic phases (D-O) and it is difficult, according to radiocarbon dates (and their error) from the sites, to precise the correlation between cultural levels and climatic peaks. Lastly, during the LGM the sea level was almost 100-120 m below the actual shoreline and in Estremadura the coast was about c. 35 km eastward (see the dynamic reconstructions of coastline between 18 Ky and present day by Dias, 2004: Fig. 2; also see our Fig. 1). The change of available land surface, especially during the Solutrean and Magdalenian, probably affected our archaeological record with disappearance of numerous sites.

During the Last Glacial, twenty-three medium to large-sized terrestrial mammal species are present in the faunal record of Portugal: eleven species of Herbivores, eleven species of carnivores and one large rodent, the beaver (Table 1). The total number of occurrence is related to the number of levels per period. Among herbivores we can strongly question the presence of the arctic genus Mammutus in Portugal, only identified by one fragmented tooth lamellae in the Middle Palaeolithic level of Gruta da Figueira Brava (Antunes, 2000). Another remain is a badly preserved shaft of long bone (femur) from Algar de João Ramos attributed to this genus exclusively on the basis of a younger radiocarbon date (14 170 +/- 330 BP) and the assumption of Elephas antiquus extinction by this period4. This last species is still known during OIS4 from isolated finds at the terrace deposits of Santo Antão do Tojal and several remains found in the Middle Palaeolithic level of Foz do Enxarrique dated around 34 Ky by U/Th (e.g., Brugal and Raposo, 1999); it is probably the last occurrence of this species in Western Europe (see Stuart, 2005). Among cervids, the fallow deer Dama dama is poorly documented with one fragmented maxillary with teeth from Mousterian levels of Gruta Nova de Columbeira and only one isolated tooth from Final Pleistocene of Algar de João Ramos (Cardoso, 1989). For carnivores, Cuon alpinus is present with only one occurrence (fragment of mandible with P4 and M1) from Middle or Upper Palaeolithic levels of Escoural (Cardoso, 1992; see also Gautier, 1996 for this cave); this species is not mentioned in the table due to problems of stratigraphical position. We have not reported sea mammals, however they are present in the Mousterian deposits of Figueira Brava (Antunes, 2000), a cave actually located in a sea cliff: one remain of ringed seal Pusa hispida and six vertebrae of common dolphin Delphinus delphis, demonstrating colder condition for this period (as the presence of the great auk Pinguinus impennis); also one find (small vertebrae) is possibly attributed to a cetacean found in the Final Gravettian of Lagar Velho (TP06, Moreno-Garcia and Pimenta, 2002).

Globally, for the last glacial the most frequent species are respectively (by decreasing abundance):

- Herbivores: red deer (C. elaphus), horse (E. caballus), aurochs (B. primigenius), and wild goat and boar (C. pyrenaica, S. scrofa);
- Carnivores: fox (V. vulpes), lynx and wolf (L. pardinus, C. lupus), brown bear and cave hyena (U. arctos, C. spelaea).

Some taxa are rare. And besides E. antiquus and Dama, it is noticeable the quasi-absence of the hemion-like horse Equus hydruntinus, occurring only during Middle Paleolithic

4 A better alternative explanation is the possible mixture of faunas of different ages, especially in what concerns this type of site, a pit-fall.
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(Pedreira das Salenmas) and Solutrean (Caldeirão, Algar de Cascais) periods; the latter co-related with the LGM. The presence of this small equid should imply dryness in climatic environment. The chamois Rupicapra is an uncommon element although present in all considered periods: it is never abundant and often is associated to hilly or high elevated sites (ex. Magdalenan of Lapa do Picareiro). Among carnivores, the archaic species Hyaena priscus was only found in the Middle Palaeolithic levels of Furninha where an important and well-preserved population is represented. The cave lion was never abundant with its last occurrence on the Early Upper Palaeolithic level of Caldeirão (27-22 000 years BP; Davis, 2002).

Throughout the last glacial sequence, the most outstanding process concern the extinction of pachyderm species (proboscid and rhinocerotid) among herbivores and large-sized predators such hyenids and felids. The taxonomic diversity, expressed in number of species per period, shows interesting features with a clear herbivore decrease between the Late Mousterian (n = 11 species) and Early Upper Palaeolithic (n = 8), due to the disappearance of pachyderms and fallow deer, and the scarcity of Equus hydruntinus and Rupicapra. The Upper Palaeolithic is marked by a relative stability in herbivore structures and then a second decrease of species by the end of Palaeolithic time with only five or six herbivore species still existing during the Holocene. Those species are temperate elements found in all southern mammal associations (Brugal et al., 2004b, c): Cervus elaphus, Capreolus capreolus, Sus scrofa, Capra pyrenaica5, Bos primigenius and Equus caballus (?); the last two species disappear at the end of Holocene or earlier.

We observe a different pattern for carnivores with a gradual decrease followed by a clear decline just after the LGM, between Solutrean and Magdalenan (see Valente, 2004, and the example of Caldeirão in Davis, 2002), and then only at the end of Upper Palaeolithic. All the large predators become extinct, both hypercarnivores (Panthera spelaea and P. pardus) and meat-bone eaters as Crocuta spelaea and H. priscus. The brown bear is not reported during Magdalenan time but it has been recognized during Holocene; this is probably related with the scarce faunal documentation for this time period, recognized in very few sites (five sites, in all with ten levels). Similar processes seem to have happened in other regions of southern Europe (e.g., Brugal et al., 2004c), where the LGM peak coincides with a strong climatic threshold in the distribution of large carnivores: reduction of range and local disappearance, before total extinction. However, the timing of this disappearance is far from uniform throughout all Western Europe, as demonstrated by evidences of cave hyena dated at c. 12 780 cal yr BP in southern Spain (Las Ventanas cave, Granada; Carrion et al., 2001) or lion in Azilian deposits dated c. 12 300 yr BP in central France (Bemilii, 2000). Finally, we can also point out the difference in timing of mammal extinctions in Portugal especially between the herbivores (preys) and carnivores (predators) the diversity diminishes at the beginning of Upper Palaeolithic for the herbivores and at the end of the same period for the carnivores. In spite of the observed diversity pattern, it is interesting to note the diminishing occupation of caves by carnivores between Middle and Upper Palaeolithic, thus suggesting a drastic change in term of competition of karstic places between carnivorous and human groups (based on %NISP Carn/Herb: Fig. 3). On the other hand, the cavities, at least those occupied both by humans or non-humans predators, are not so numerous and often have small dimensions (as expressed by the terms “Lapa” or “Buraca” which mean respectively small and less deep rockshelter, and burrow or hole), or narrow galleries. Therefore, if modern human groups still actively seek cavities in their settlement system, complementary to the several open air localities, it seems that carnivores avoid systematically such places.

In order to detail the change in mammalian associations, data have been expressed according the percentage of occurrence, individually for herbivores and carnivores. The Table 2 indicates the most frequent taxa ranked by abundance from 1 to 4. The red deer is always dominant, accompanied by horse during the Solutrean, thus indicating the coldest conditions for the entire last glacial. The herbivore fluctuations demonstrate the tendency of global climatic changes; ranking modifications for wild goat and aurochs, beside the association deer/horse, are clear evidences toward gradual colder environment from Mousterian to Solutrean. The main difference appears during the Magdalenan with more temperate species as boar and aurochs in detriment of horse and wild goat, probably related to deglaciation process and climatic improvement. With lower percentages, chamois and roe deer are also present, generally found in different levels and probably more associated with local environment, namely elevation and/or protected forested areas (“refugium”). Changes in carnivore compositions seem relatively more spectacular due to the disappearance of several species (cf. above), especially the large predators often considered humans’ direct competitors. Given the data, the most interesting and logically phenomenon, is the increase of lynx followed by wolf and fox, all predators of small game like leporids. From the Early Upper Palaeolithic, the trio lynx/wolf/fox becomes predominant.

Interestingly in the same time period prehistoric people become more involved too into small game acquisition and we can enquire about the importance of competition between humans and medium to small carnivores for this type prey. This pattern can explain also the lower degree of carnivore occupation in caves as seen previously.

5 Capra ibex or caucasica in other parts of Europe; Capra ibex and aegagus in Eastern Mediterranean.
The animal communities are relatively homogenous during the Last Glacial (OIS 4-2) in Central Portugal, especially for herbivores with persistence of temperate species as red deer and aurochs, horse and wild goat in the fossil record. Climatic oscillations, in relation with latitudinal and altitudinal shifts, result in modifications on the proportion of species, and subtle variations can be seen for the upper pleni-glacial and late glacial. Amongst carnivores, the disappearance of large predators constitutes the main feature happening just after the last cold maximum (LGM). It is important to notice the total absence of cold adapted species as reindeer, bison, musk ox, saiga, mammoth, woolly rhino, arctic fox, wolverine, as well as giant deer (Megaloceros) and cave bear (Ursus spelaeus), when compared with northern region of Iberia (e.g., Cantabria). However these species were never common in the Iberian mammal associations (except cave bear well represented in the mountain range of Pyrenees) and seem absent in the rest of the peninsula, with the notable exception of a mammoth (M. primigenius) found in a peat-bog near Granada (Padul dated to 35 790+/−960 BP, OIS 3) and woolly rhino (C. antiquitatis) from a terrace deposit near Madrid (Arroyo Culebro, attributed to early Würm, OIS 4?) (Garcia and Arsuaga, 2003). A clear biogeographic shift seems to occur in Iberia peninsula during the Last Glacial with northern region subject to colder condition (cf. the model of “Ebro frontier” of some authors), more or less like the one existing today, which indeed reflects both climate and vegetation zones (oceanic/eurosiberian versus mediterranean/submediterranean regions), which we can add the mountain climate. It seems obvious that climatic conditions were relatively severe during at least the upper pleni-glacial in Portugal, enough to develop grass steppes and dispersed open forest but without bringing important changes in global mammal associations. The southern part of Iberia was never a deserted herbivore ecosystem for the Last Glacial, but this picture issued from many sites in Central Portugal could be a little different in other part of the country’s territory, especially in northern areas.

Another determinant aspects concern specific processes involving large mammalian associations in Portugal. The first one represents the survival of species in comparison with other west European faunas. The most noteworthy is the persistence of straight-tusked elephants (E. antiquus, Brugal and Raposo, 1999), archaic hyenids (H. prisca) and wolf (the small form C. lupus lunellensis) from early last glacial levels of Furninha (Cardoso, 1993), along with other species as rodents (A. cantiana from Mousterian levels of Figueira Brava; Jeannet, 2000) or Neanderthals, until the beginning of the Last Glacial. Moreover, endemic processes are acting on species, which present smallest size and slenderer elements in comparison with northern populations. Cervids and caprids are probably affected by this process and will need complementary studies, as the one made on equids, which lead to the description of the new sub-species Equus caballus antunesi (Cardoso and Eisenmann, 1989) from the early last glacial of Pedreira das Salemas and Gruta das Fontainhas, and still recorded in a later phase at Algar de João Ramos (see footnote 3).

CONCLUSIONS

In the last decade, new archaeological excavations and studies of old collections according to modern taphonomic and zooarchaeological perspectives allowed new results about the mammal associations supported by precise cultural layers and numerous isotopic dates. We can then propose a comprehensive database about medium to large mammals covering the Pleistocene/Paleolithic in the Portuguese territory, set upon 55 sites and around 75 levels, and concerning 23 species.

The fossil record is scant for Lower Pleistocene, and still rare for Middle Pleistocene and the beginning of Upper Pleistocene. However we can point out the very important documentation from the Middle Pleistocene site of Galeria Pesada with an original association and the rich information for the period between late Middle Paleolithic and final Upper Paleolithic, with many sites located in Central Portugal.

The Last Glacial is a complex period in term of climate, well known now from high resolution data from deep-sea core located not far from the coast of Portugal (SU 8118, SO 75-26KL, MD 95-2042, e.g., Sanchez-Goni et al., 2000; Turon et al., 2003). Past climatic fluctuations had clear impact on land paleoenvironment on southern regions as Iberia peninsula and Atlantic coast. We have organized our data for culturally time periods more or less bracketed between main cold events (Heinrich) in the last 40 Ky, thus allowing the appreciation of dynamics in herbivore and carnivore distributions. The repeated cold events of relatively long duration (1000-2000 years) have some incidence on mammal ecological structure, at least in the variation of population density connected with more or less efficient rate of reproduction. To some degree, large mammalian association reproduce small-scale environmental and climatic oscillations within the last glacial. In Portugal, minor changes have been observed concerning the composition and the frequencies of species association, marked by local carnivore extinctions and by a relative stability among the herbivore communities without any cold-adapted species known in other part of Western Europe and limited to northern Iberia. The main change occurs at the end of Upper Pleistocene, during the development of Magdalenian culture, with the establishment of distinct mammalian populations. The Portuguese specificity is also shown with evolutive and endemic processes, related to biogeographical factors.

This is also a complex period regarding hominid strategies, as noticed in two major facts like the replacement of last
Neanderthal groups by anatomically modern humans and the enlargement of diet with active acquisition of small game during the Upper Palaeolithic, particularly the terrestrial one as the leporids. The knowledge about past animal dynamics, related or not to climate, constitutes a relevant question in the actual debate about settlement patterns, adaptation and fitness of human species and nature of game acquisition s.l. by prehistoric people.

**BIBLIOGRAPHY**


6 And probably contact, if we accept the hypothesis of crossbreeding for the Gravettian child of Lagar Velho (Zilhão and Trinkaus, 2002).


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### TABLE 1. Number of occurrence of Mammal species during the Last Glacial in Portugal.

<table>
<thead>
<tr>
<th>OIS</th>
<th>MP (n = 20)</th>
<th>EUP (n = 15)</th>
<th>PS + S (n = 12)</th>
<th>Ma (n = 10)</th>
<th>Holocene</th>
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<td>4/3</td>
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<td><strong>Herbivores</strong></td>
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<td>+</td>
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<td>10</td>
<td>10</td>
<td>+</td>
</tr>
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<td>2</td>
<td>2</td>
<td>+</td>
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* Dama: one single remain.
MP = Middle Paleolithic; EUP = Aurignacian + Gravettian; PS + S = Protosolutrean + Solutrean; Ma = Magdalenian; OIS = Oxygen Isotopic Stage.
TABLE 2. Ranking distribution of taxa in Middle and Upper Paleolithic of Portugal (based on % occurrence per time-period).

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<td>Ma (n = 10)</td>
<td>Cervus</td>
<td>Sus</td>
<td>Bos</td>
<td>Equus</td>
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<tr>
<td>PS + S (n = 12)</td>
<td>Cervus / Equus</td>
<td>Capra</td>
<td>Bos / Sus</td>
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<tr>
<td>EUP (n = 15)</td>
<td>Cervus</td>
<td>Equus</td>
<td>Capra</td>
<td>Sus</td>
</tr>
<tr>
<td>MP (n = 20)</td>
<td>Cervus</td>
<td>Equus</td>
<td>Bos</td>
<td>Capra</td>
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<tr>
<td></td>
<td>Carnivores</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ma (n = 10)</td>
<td>Lynx</td>
<td>Canis / Vulpes</td>
<td>Felis</td>
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</tr>
<tr>
<td>PS + S (n = 12)</td>
<td>Lynx / Vulpes</td>
<td>Canis</td>
<td>Ursus / Crocuta / Felis</td>
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<tr>
<td>EUP (n = 15)</td>
<td>Vulpes</td>
<td>Canis / Lynx / Crocuta</td>
<td>Ursus</td>
<td></td>
</tr>
<tr>
<td>MP (n = 20)</td>
<td>Ursus</td>
<td>Canis</td>
<td>Lynx / Vulpes / Crocuta / P.pardus</td>
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</table>
Dynamic of large mammalian associations in the Pleistocene of Portugal

FIGURE 1. Location of Middle and Upper Palaeolithic/Pleistocene sites in Portugal (synthetic view), with line seashore at 18 Ky (after Dias et al., 2000).

FIGURE 2. Dated-sites (± 1σ radiocarbon date, uncalibrated BP) of Middle and Upper Palaeolithic sites with faunas in Portugal (see table 1 for abbreviations); H = Heinrich events, YD = Younger Dryas.
Dynamic of large mammalian associations in the Pleistocene of Portugal

FIGURE 3. Mean Percentage of Carnivore versus Herbivore (based on NISP) in various cave sites of Middle and Upper Palaeolithic in Portugal and number of medium-large predators (curve: *C.lupus*, *U.arctos*, *C.spelaea*, *P.spelaea*, *P.pardus*, *L.pardina*).