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BIOGEOGRAPHIC ANALYSIS OF UPPER PLEISTOCENE FELID (*FELIS*, *LYNX* AND *PANTHERA*) REMAINS IN ARCHAEOLOGICAL SITES ON THE IBERIAN PENINSULA

This paper will point out the geographical distribution of the felid family (*Felis, Lynx and Panthera*) bone remains in archaeological sites on the Iberian Peninsula during the Upper Pleistocene. These depositional contexts are located in caves or rock-shelters during the Upper Pleistocene, which were alternatively occupied, by both carnivores and hominins.

Before examining the presence of these species in depth on the Iberian Peninsula, some considerations must be made. Firstly, bone remains are only preserved in determinate geological contexts; and in multiple regions, karstic depositional contexts (caves, rock-shelters and potholes) have preserved bone remains. Secondly, in some regions during the 20th century the research on Palaeolithic archaeology and Quaternary palaeontology, in addition to the development and constitution of speleological groups and the exploratory work on multiple karstic systems, was encouraged. The outcome being the discovery and excavation of multiple archaeological and palaeontological remains, especially post 1970s with the appearance of specialists in zooarchaeology.

The chronological framework of this study is the Upper Pleistocene. This period begins in Western Europe with the Eemian interglacial (OIS 5e) 126 000 ± 5000 years ago and ends with the early Holocene (OIS 1), 9700 years ago. The Upper Pleistocene was dominated by the glacial phase of Würm (OIS 4, 3 and 2). Southwestern Europe was in general cold with irregular phases of warmer (interstadial) and colder (stadial) periods. During these cold periods, a continental ice sheet covered Northern Europe, and an area called the frozen desert became an unoccupied/unpopulated space. On the other hand, the southern peninsulas with milder climatic conditions were never unoccupied. The Iberian Peninsula became a climatic and geographical refuge (Sommer/Nadachowski 2006).

In this study, eight felid species have been included: the lion (*Panthera leo spelaea, Panthera leo clueti* and *Panthera* sp.), leopard (*Panthera pardus*), lynx (*Lynx lynx, Lynx pardina* and *Lynx spelaea*) and the wildcat (*Felis silvestris*). Traditionally, taxonomic classifications were done following palaeontological parameters and chrono-cultural adscription of the sedimentary contexts. Nevertheless, the identification process has evolved, and two lion forms have been identified, the cave lion (*Panthera leo spelaea*), a large carnivore often discovered in the oldest Upper Pleistocene layers, while in the younger layers a much smaller lion (*Panthera leo clueti*) appeared, and was comparable in size to the modern African lion (Castaños 2005).

Nowadays, ancient DNA analyses are providing tremendous advances in the taxonomy. During the last decade, the existence of two lion species (*Panthera leo spelaea* and *Panthera leo clueti*) has been put in doubt (Burger et al. 2004; Ersmark et al. 2014). At present, it is assumed that the Pleistocene lion decreased in size during the Upper Pleistocene, until its final extinction process at the end of the Pleistocene and eventual replacement by the European subspecies of African lion (*Panthera leo*).

The second example is the taxonomical ascription of lynx remains. Three species were identified (*Lynx lynx, Lynx spelaea* and *Lynx pardina*) on the Iberian Peninsula. In this case, the geographical location and size were fundamental to classify some of the remains as belonging to one or the other taxa. During previous

In: Nicholas J. Conard · Henning Hassmann · Kurt Felix Hillgruber · Jordi Serangeli · Thomas Terberger (eds), The *Homotherium* Finds from Schöningen 13II-4. Man and Big Cats of the Ice Age. Forschungen zur Urgeschichte aus dem Tagebau von Schöningen 4 (Mainz 2022). DOI: https://doi.org/10.11588/propylaeum.1006.c13523

decades, DNA has determined clarified taxonomic adscriptions. In 2015, the presence of the European lynx has been confirmed (*Lynx lynx*) in the Cantabrian Mountain range (northern Iberia). Furthermore, a genetic link between the Iberian lynx (*Lynx pardina*) and the Pleistocene lynx (*Lynx spelaea*) has been established (Rodriguez-Varela et al. 2015a). The Pleistocene lynx and the Iberian lynx should form a single species. The Iberian lynx evolved and adapted as a reaction to colder environments. Furthermore, the biogeographic distribution of this species spread towards the end of the Pleistocene into Southern France and Northern Italy (Rodriguez-Varela et al. 2015b).

Finally, we must address the provisionality of this paper, as in much bibliographic research, there arises the possibility that maybe some of the more obscure papers have not been cited and this is therefore incomplete. Older studies and palaeontological discoveries have not been systematically published. Decades ago, the recovery of bone remains in caves was often not even reported. These collections were kept in boxes, remaining unpublished or only mentioned in short reports. Because of this situation, it became very hard to recompile information. Fortunately, this situation has changed immensely since the 1970s, with the emergence of well-structured institutions in Spain and Portugal (departments of prehistory, natural sciences associations, museums, etc.) and the first researchers specializing in zooarchaeology slowly but surely started to achieve systems and a structured order in the conservation and recovery of finds.

Most of the felid bone remains identification was done on Pleistocene archaeological sites. During the early Upper Pleistocene, a large number of caves used as refuges and dens, with shared occupation between carnivores and hominins (Villaluenga 2016a; 2016b). Later, and in particular during the Upper Palaeolithic, the presence of smaller taxa (*Lynx* and *Felis*) on archaeological sites was linked with fur/hide exploitation or meat consumption (Yravedra 2005). The continual appearance and the absorption of new evidence of felid remains at Upper Pleistocene archaeological sites has improved the collection and compilation of information and made it state of the art.

DISCUSSION

Geography

The Iberian Peninsula is the westernmost of the three major Southern European peninsulas (Iberian, Italian and Balkan). It is bordered to the South and East by the Mediterranean Sea and on the Southwest, West and North by the Atlantic Ocean. In the Northeast the Pyrenees mountains (Aneto, 3404 m a. s. l.) separate the Iberian Peninsula from the rest of the continent, the Strait of Gibraltar separates the southern Iberian tip from Africa (Ceuta, Spain). The Iberian Peninsula extends from the southernmost extremity to the northernmost extremity over a distance of 865 km and from the easternmost to the westernmost point; the distance is approx. 1155 km. Altogether the Iberian Peninsula is surrounded by 3313 km of coastline. During the Last Glacial Maximum (LGM), this shoreline was a minimum of -115/-120 m lower than the current coastline.

The Iberian Peninsula is after the European Alps the region with the highest number of peaks. Three quarters of the Iberian Peninsula consists of a high plateau known as the »Meseta Central« ranging from 610 to 760 m in altitude. This plateau is surrounded by multiple mountain ranges where most of the main river sources are located (main rivers are Miño, Duero, Tajo, Guadiana, Guadalquivir, Segura Júcar and Ebro), which find their way to the sea through geological gaps eroded in between mountain ranges (Vera Torres 2004).

The Iberian Peninsula Mountain ranges contain rocks of multiple ages, from Ediacaran (635 Ma) to Quaternary (2.5 Ma to recent) and almost all kinds of rocks are represented, the Iberian Massif is considered to be

Fig. 1 Wildcat (*Felis silvestris*) biogeographic distribution on the Iberian Peninsula. Site numeration follows **tabs 1-4**. – (Map A. Villaluenga).

the core of the peninsula, it is composed of Mesozoic and Tertiary cover rocks. The northeastern Pyrenees and the southeast Baetic mountain range are part of the Alpine belt. Northward movement of the African tectonic plateau created these elevations. Finally, the western side formed by magmatic substrate formed by the Atlantic Ocean opening process. Erosion has produced multiple forms of evaporate and carbonate Palaeozoic, Mesozoic and Cenozoic rocks (Durán-Valsero/Robledo-Ardilla 2009). This substrate has been karstified, creating multiple forms, including caves and rock-shelters occupied by carnivores and hominins during the Pliocene and Pleistocene (Jordá-Pardo 2009).

Ethology and phylogeny

Wildcat (*Felis silvestris*)

The wildcat (*Felis silvestris*) is the smallest felid in Europe; males (7.5 kg) are bigger than females (5 kg). The actual distribution begins in the East in the Caucasus and continues onto the southern Iberian Peninsula in the West. Actually in the Iberian Peninsula two subspecies are identified, *Felis silvestris silvestris* in the North and

Felis silvestris tartessia in the Mediterranean and southern areas. The latter subspecies is larger and has a more contrasted coloration. This species lives in forested environments where it is able to find multiple resources and refuge. This animal has a heterogeneous diet including small mammals, birds, fish, amphibians and insects, with rabbit as its main prey on the Mediterranean coast. The wildcat has a solitary, nocturnal and territorial behaviour. This is one of the main reasons for it not to be a very well-known species (Macdonald/Barrett 2002). During the Upper Pleistocene, the wildcat is present on the whole Iberian Peninsula. It has been identified at 53 archaeological sites, from the Cantabrian Mountain range in the North to Gorham's Cave (Gibraltar) in the south including multiple sites on the Mediterranean (11) and Atlantic coasts (10) (**fig. 1; tab. 1**).

Lynx (*Lynx pardina, Lynx spelaea, Lynx lynx* and *Lynx* sp.)

There are two species of lynx in Europe: in southern Spain and Portugal the Iberian lynx, Pardel lynx or Spanish lynx (*Lynx pardinus*). This species is smaller (9-13 kg) than the European lynx (*Lynx lynx*) (males 18-30 kg and females 8-21 kg). The Iberian lynx is a specialized rabbit hunter. Its current habitat is an open forested Mediterranean environment. A high degree of specialization has put the species on the brink of extinction, with the present population fluctuating around 300 individuals, making it one of the most endangered carnivore species in the world. The European lynx (*Lynx lynx*) lives from Atlantic coast to the Taiga forests and mountains up to a height of 3400 m a. s. l. Its diet is broad, including small prey up to small and medium-sized subadult ungulates (Macdonald/Barrett 2002).
For the Upper Pleistocene a third species described in the Iberian and Southern European fossil record, the Pleistocene lynx or cave lynx (*Lynx spelaea*). The body size of this species was in between the European and the Iberian lynx. The first palaeontological description of this species made employing skeletal remains discovered at Grimaldi (Boule 1919) and L'Observatoire (Boule/de Villeneuve 1927) caves (Monaco). However, only in the 1980s was it officially accepted as being a distinct species. Finally, DNA analysis has proved a direct genetic link between the Iberian lynx (*Lynx pardinus*) and the Pleistocene lynx (*Lynx spelaea*) (Rodriguez-Varela et al. 2015a). Following the most recent information it considered as a single species, nevertheless for this paper we have kept the distinct nomenclature for both forms (**fig. 2**). The Iberian lynx distribution was wide, including the Iberian Peninsula, the French Mediterranean coast and Northern Italy during the late Upper Pleistocene and early Holocene.
European lynx (*Lynx lynx*) was identified for the first time during the 1980s in the southern Pyrenees at the Upper Palaeolithic archaeological sites Rascaño (prov. Cantabria/E; González-Echegaray/Barandiarán 1981) and Erralla (prov. Gipuzkoa/E; Altuna/Baldeon/Mariezkurrena 1985). Later on, more remains were identified on the Mediterranean coast. The Ebro River Valley acts as a natural boundary for this species (**fig. 3**).

Leopard (*Panthera pardus*)

The presence of leopard (*Panthera pardus*) remains on the Iberian Peninsula begins during the Middle Pleistocene and appeared regularly in archaeo-palaeontological contexts until the end of the Upper Pleistocene (**fig. 4**). The extinction of the Pleistocene leopard came during the Magdalenian (climatic phase Würm IV) and early Holocene (Castaños 1987; Sanchís et al. 2015) as the most probable causes of extinction mentioned are the climatic changes and the changes in the leopard prey population.
To try to have an idea of what this extinct leopard was like, we must look at the actual single leopard living presently in the northern environments, the Amur leopard (*Panthera pardus orientalis*). This species lives

Fig. 2 Iberian lynx (*Lynx pardinus,* in yellow) and Pleistocene or cave lynx (*Lynx spelaea,* in red) biogeographic distribution on the Iberian Peninsula. Site numeration follows **tabs 1-4**. – (Map A. Villaluenga).

in Eastern Siberia. Its body size should be similar to the Pleistocene European leopard (31-70 kg), with a length up to 190 cm and a height of 80 cm. Quite exceptionally this subspecies has two furs, one for winter (7 cm) and one for summer (2 cm) the last one being more colourful. Leopards have preferential nocturnal behaviour; during the day they usually rest in rock-shelters, caves or on tree branches.

The leopard is a solitary ambush hunter. Ethological sources have documented that sometimes they would bring their prey carcasses to caves and rock-shelters to protect them from scavengers, these refuges are also used as dens (Ruiter / Berger 2000). This behaviour should be present in European Pleistocene leopards, some Upper Pleistocene archaeozoological assemblages have been interpreted as leopard consumption sites, characterized by middle size ungulate remains, in particular ibex and chamois (Yravedra 2007a).

Lion (*Panthera spelaea* and *Panthera leo clueti*)

The cave lion is one of the most popular species of the Eurasian Prehistory. During decades of work on the fossil record, two subspecies of lion have been identified: *Panthera leo clueti* with a body size similar to modern-day lions (> 200 kg) and the larger *Panthera spelaea goldfuss* (Ballesio 1980). Actually, this dis-

Fig. 3 European lynx (*Lynx lynx* in yellow) and indeterminate lynx (*Lynx* sp.) biogeographic distribution on the Iberian Peninsula. Site numeration follows **tabs 1-4**. – (Map A. Villaluenga).

tinction attributed to a size reduction through the Upper Pleistocene: older animals were larger than the younger individuals were, these should be comparable to actual African lions (Burger et al. 2004). Some other authors consider that these size differences are due to sexual dimorphism (Turner 1984), as extant male lions are 30 % larger than females.

For decades the origins of the large felids was not clear. Nowadays, most of the researchers consider that the most probable hypothesis is that 4.5 million years ago *Panthera gombaszoegensis* was the ancestor of the lion, tiger, leopard and jaguar. Lion (*Panthera leo*) and cave lion (*Panthera spelaea*) evolved from the first lion species (*Panthera leo fossilis*), appearing around 3 million years ago in Eastern Africa. The direct ancestor of the cave lion migrated to Eurasia 900 000 years ago. Since then, the European and African lions have evolved independently in four populations: the African lion (*Panthera leo*), the cave lion (*Panthera spelaea*) the Asiatic lion (*Panthera leo persica*) and the American lion (*Panthera leo youngi*). Last one migrated to North America during the Middle Pleistocene (400 000-300 000 years ago) and evolved in the Upper Pleistocene *Panthera leo atrox* (Barnett et al. 2009; Ersmark et al. 2014). During the early Holocene in Southern Europe, after the extinction (10 000 years ago) of the cave lion (*Panthera spelaea*) (Stuart/Lister 2011), Europe was colonized by another lion subspecies (*Panthera leo europaea*), who maybe originated from African or Persian lion population. Maybe this subspecies has been identified

Fig. 4 Leopard (*Panthera pardus*) biogeographic distribution on the Iberian Peninsula. Site numeration follows **tabs 1-4**. – (Map A. Villaluenga).

as *Panthera leo clueti* in southwestern European late Pleistocene and early Holocene archaeological and palaeontological contexts.

Further analysis is necessary in this aspect. This last European lion (*Panthera leo europaea*) colonized Southwestern Europe, from the Iberian Peninsula (**fig. 5**) to the Balkans, being a popular prey amongst the Greeks and Romans, the over-hunting of this animal (100 AD) led to its extinction on the Balkans.

The cave lion's (*Panthera spelaea*) external appearance is still uncertain; Upper Palaeolithic art has been for a while the single source of information. Chauvet Cave (dép. Ardèche/F) contains a whole set of lion representations, but not including the male lions characteristically mane. This is the case in some other caves as Combarelles (dép. Dordogne/F), Armintxe (Lekeitio, Biscay/E) or Vogelherd (Swabian Jura/D) among others. However, the absence of this feature is usual in the Indian lion (Azemá 2009; 2010). The ethology of this species is unknown, single living examples are Indian (*Panthera leo persica*) and African lions (*Panthera leo*), both live in groups, composed of females, cubs and one or two dominant males. They defend a well-defined territory, located in open forested spaces. The diet of lions is composed of middle-sized ungulates and in Africa occasionally by megafauna. Scavenging is also a recurrent behaviour. The cave lion (*Panthera spelaea*) was a powerful hunter, probably in direct competition with the cave hyena (*Crocuta crocuta spelaea*) and hominins. Isotopic analyses has revealed a diet composed of horse, bison, aurochs, red deer

Fig. 5 Biogeographic distribution of lion on the Iberian Peninsula. European late Pleistocene and early Holocene lion (*Panthera leo clueti* in yellow), cave lion (*Panthera spelaea* in red) and indeterminate lion (*Panthera* sp. in blue). Site numeration follows **tabs 1-4**. – (Map A. Villaluenga).

and Pleistocene megafauna, as the giant-deer or subadult woolly rhinoceros and mammoth (Bocherens et al. 2011).

Spatial distribution

Most archaeological sites on the Iberian Peninsula are located within karstic contexts. This geological context is chemically dissolved by water creating multiple forms and orifices as caves and rock-shelters. These structures inhabited during the Pleistocene by hominins and carnivores, the following lines will present the location of felid remains across the Iberian Peninsula.

As mentioned, remains preservation is linked to multiple factors: First, the geology and the distribution of appropriate substrates. Second, the biogeographic distribution of the species. For example, some species populated the entire territory, while the European lynx (*Lynx lynx*) and cave lion (*Panthera spelaea*) were restricted to the northern and central areas. Third, the archaeological field work tradition, the influence of the first French researchers on prehistoric archaeology as they introduced this discipline at the end of the

19th century and the early 20th century. Fourth, the preservation of bone remains. Organic remains on the Iberian Peninsula are only preserved in exceptional circumstances, fluvial-lacustrine and karstic contexts (Sala-Ramos et al. 2014). Considering these criteria, it should be possible to correct the overrepresentation of northern Iberia sites comparing to the rest of the peninsula.

The spatial distribution of felids (*Felis silvestris*, *Lynx lynx*, *Lynx pardinus*, *Lynx spelaea, Panthera pardus, Panthera leo, Panthera spelaea* and *Panthera* sp.) shows differences. Some taxa like the wildcat (*Felis silvestris*), the Iberian lynx (*Lynx pardinus*) and the leopard (*Panthera pardus*) are present over the whole peninsula. On the other hand, the distribution of the European lynx (*Lynx lynx*) is restricted to the northeastern Cantabrian region. Lions (*Panthera spelaea* and *Panthera leo*) are restricted to the northern half of the Iberian Peninsula. A limited distribution to Northern Iberia is not exclusive to these species: the distribution of reindeer, woolly rhinoceros, mammoth (García/Arsuaga 2003), cave bear (Villaluenga 2009), arctic fox (Altuna/Mariezkurrena 2004) and wolverine (Altuna 1963; Altuna/Baldeón 1986) is limited to the northern part of the peninsula. This model of distribution could be related to climatic and environmental conditions, linking the northern part of the Iberian Peninsula to the Upper Pleistocene and glacial, non-analogue continental environments. In contrast, warmer conditions should be present in the Mediterranean area and the southern part of the peninsula.

In total, 143 archaeological sites have been analysed. To understand the different regional patterns, the Iberian Peninsula have been divided into five different regions: Cantabrian Corniche, Centre and Pyrenees, Mediterranean coast, South and West. The Cantabrian Corniche with a geological substrate composed of carbonate massifs has the highest number of sites (57) and quantitatively the highest number of bone remains and species. Furthermore, a long tradition of Quaternary palaeontology and prehistoric archaeology has helped to encourage multiple excavation projects and zooarchaeological analysis, including regional biogeographic and chronologic analysis (Altuna 1992a; 1992b; Castaños 1987; 2005) (see **tab. 1**). The Central Iberian Peninsula and Pyrenees were peopled since the early Upper Pleistocene, however, the Pleistocene deposits containing organic remains are few (18) because the preservation in this region only occurred in rock-shelters or caves (**tab. 2**; Blasco-Sancho/Montes/Utrilla 1996; Yravedra 2007b; Sauqué et al. 2014). The Mediterranean coast is revealing more and more archaeological accumulations (40), due to a systematic analysis by multiple research teams (**tab. 3**; Estévez 1979; Sanchís 2015; Sanchís et al. 2015). The southern region is considered an exceptional territory with very diverse environments, from the dry Mediterranean and Atlantic coastal lines to high altitude occupations in the Baetic Massif (**tab. 4**; Barroso et al. 2014; Finlayson et al. 2014). In this region, only ten excavated sites show the presence of bone remains covering four separate felid species. Finally, the western region (17) has an intense site concentration around the Tajo River mouth (**tab. 4**; Cardoso 1993). On the Iberian Peninsula the wildcat (*Felis silvestris*) has been identified at 53 sites, the lynx (*Lynx lynx, Lynx spelaea* and *Lynx pardinus*) has been found at 80 sites, the leopard (*Panthera pardus*) at 76 sites and the lion (*Panthera spelaea, Panthera leo* and *Panthera leo* sp.) at 31 sites.

An individualized comment is required for each species. Firstly, *Felis silvestris* is present over the whole Peninsula, being represented at 53 sites (**fig. 1**). However, remains are more frequent in the Cantabrian Corniche (21) when compared with the remaining regions, but considering the percentage as a reference, the western region is the area with a higher (58 %) concentration of wildcat in its faunal assemblage.

Lynx (*Lynx pardinus, Lynx spelaea, Lynx lynx* and *Lynx* sp.) split into two figures: includes the Iberian lynx (*Lynx pardinus*) and the Pleistocene lynx (*Lynx spelaea*) (**figs 2-3**). As previously mentioned, both are currently considered two morphotypes of a single species (Rodriguez-Varela et al. 2015a). The presence of the Iberian lynx recorded at 57 sites; the highest frequency documented in the northeastern region (16 sites) and the northern Mediterranean coast (14 sites). The Iberian lynx (*Lynx pardinus* and *Lynx spelaea*) is present

over three quarters of the peninsula, its absence from the northwestern area could be biogeographically and palaeoenvironmentally significant.

European lynx (*Lynx lynx*) and indeterminate lynx (*Lynx* sp.) remains are restricted to the eastern half of the Iberian Peninsula (**fig. 3**). First taxa has a northern distribution (Cantabrian Corniche and Mediterranean coast) being present on the Iberian Peninsula during cold climatic phases (García/Arsuaga 2003). The European lynx colonized the Cantabrian region with a higher density in the eastern area (8) than in the central (5) and western (1) areas. On the eastern extreme of the Iberian Peninsula, seven sites have reported presence of this species, and actual data shows that the Ebro River acts as a natural boundary to the spatial distribution of the European lynx on the Iberian Peninsula. However, a single exception must be reported in Cova del Corb (Ondara, prov. Alicante/E). This taxonomic determination should be confirmed. Indeterminate lynx remains published from 20 archaeological sites, most of them on the Mediterranean coast (10), the southern extreme (4), the central mountain range (2) and finally three sites in the Cantabrian Corniche. To conclude with this general distribution, a total absence of lynx bone remains in archaeological sites on the northwestern peninsula must be mentioned, an area with few archaeological records but including leopard (*Panthera pardus*) and lion (*Panthera leo* sp.) remains.

Large felids are also present on the Iberian Peninsula: the leopard (*Panthera pardus*) was the carnivore with the highest number of recovered remains and was present on 76 archaeological sites (**fig. 4**). In two of the regions, the leopard identified in one-third of all archaeological sites: 26 sites (36 %) in the Cantabrian Corniche and 22 in the Mediterranean region (35 %). On the other hand, in the centre of the Iberian Peninsula and the Pyrenees, the leopard (*Panthera pardus*) has been identified at eleven sites (61 %), followed by seven sites in the southern area (70 %) and western region (58 %). As mentioned before, maybe the repetitive presence in karstic contexts should be related to the ethology, as the leopard probably was a solitary ambusher, specializing in medium and small size ungulates. Bone remains, gnawed by leopards were identified as ibex (*Capra pyrenaica*) and chamois (*Rupicapra pyrenaica*) (Yravedra 2007a), typical species for rocky biotopes.

Lion (*Panthera leo clueti, Panthera spelaea* and *Panthera* sp.) is the largest and least represented carnivore in the Iberian Peninsula (36 sites) (**fig. 5**). *Panthera leo clueti* (9) and *Panthera spelaea* (7) have been identified in the Cantabrian Corniche (Castaños 2005). Taxonomic differentiation based on body size, as *Panthera spelaea* was larger than any actual felid. For a while, *Panthera leo clueti* has been considered as a modern species incoming during the late Upper Pleistocene, which survived until the early Holocene. However, DNA analysis has revealed a genetic relation between both Upper Pleistocene lions. Nowadays, most of the researchers agree on the existence of a gradual size diminution through time. If this is correct, *Panthera spelaea* and *Panthera leo clueti* should be considered as a single taxa, known as *Panthera leo spelaea* (P. Fosse, personal communication). Later, after the extinction of this species (Stuart/Lister 2011) a modern lion, the European subspecies (*Panthera leo europaea*) colonized Southern Europe up until the early Holocene.

Over the rest of the Iberian Peninsula, the lion has been identified as *Panthera* sp. or *Panthera leo* sp. in 20 archaeological sites, apparently this taxa was missing in Southern Iberia, the southernmost distribution reached the Tajo River mouth (Gruta do Escoural; prov. Alentejo/E) in the West and Cap del Nau (Cova Negra; prov. Alicante/E) in the East. Nevertheless, in Central Iberia, the Central Massif (Cueva de los Casares and Jarama VI [both prov. Guadalajara/E]) is considered the natural boundary of the biogeographic distribution of *Panthera leo* sp. or *Panthera* sp.

CONCLUSIONS

In this paper I have analysed felid (*Felis silvestris, Lynx pardinus, Lynx lynx, Lynx* sp.*, Panthera pardus, Panthera leo clueti, Panthera spelaea* and *Panthera* sp.) presence in 143 archaeological sites on the Iberian Peninsula during the Upper Pleistocene. This study provides a preliminary view on felid biogeographic distribution.

Overall, it is possible to identify a heterogeneous site distribution, linked to the presence of the appropriate geological substrate to provide refuges, rock-shelters and caves. These areas are mainly located in karstic areas near coastlines. Differences in felid presence is also related to the ecological and climatic preferences of each species. The Iberian lynx (*Lynx pardinus*) is a specialized rabbit and small prey hunter. Its population and eventual presence in a region related to the distribution of prey. However, the Pleistocene lynx (*Lynx spelaea*) distribution was restricted to the northern half of the peninsula. This difference in biogeographic distribution could be related to recent (end of the Upper Pleistocene) adaptations, specialization and body size reduction to warmer and dryer environmental conditions.

Also taxa not represented on the full territory, such as the European lynx (*Lynx lynx*) and lion (*Panthera leo clueti, Panthera [leo] spelaea* and *Panthera* sp.), should be related to multiple degrees of adaptation to/in colder environments. The distribution area of the European lynx just reaches the Cantabrian Corniche and the Northern Mediterranean coast, while lion remains extend to the southern third of the Iberian Peninsula.

Finally, biogeographic analysis should become a powerful tool used to make interpretations in prehistoric and quaternary environmental analysis. However, these studies are in a state of constant evolution and this paper has been focused on a single family. In the future, this type of study should be extended to include large and small mammals. Furthermore, new analyses will provide data able to answer certain questions, such as the reasons for the absence of certain taxa in some areas of the region. The Iberian Peninsula, a relatively restricted geographical region revealed a complex territory, with multiple environments and geographic conditions. These factors have provided the geographic overlap of species adapted to various different conditions making the Iberian Peninsula a unique region for the analysis of faunal adaptations to climatic changes.

ACKNOWLEDGEMENTS

This research was possible thanks to Basque Government PhD Research Grant Program funding, High yield research group on Prehistory (IT-1223-19) University of the Basque Country (Vitoria-Gasteiz, Spain) (aritza.villaluenga@ehu.eus), Aranzadi Sciences Society (Saint Sebastian, Spain) and MONREPOS Research Centre and Museum for Human Behavioural Evolution-RGZM, the support. – Finally, I would like to acknowledge Felix Hillgruber and PALÄON team for the invitation to the *Homotherium* workshop.

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SUMMARY / ZUSAMMENFASSUNG

Biogeographic Analysis of Upper Pleistocene Felid (*Felis*, *Lynx* and *Panthera*) Remains in Archaeological Sites on the Iberian Peninsula

This paper aims to introduce the biogeographic distribution of felids (*Felis, Lynx* and *Panthera*). The analysed period is within the last glacial phases. This period was quite unstable, changing climatic conditions affected mammals biogeographic distribution. I would like to focus this analysis on the Iberian Peninsula, the southwestern most region of Europe. However, it is a complex geography with different climatic areas affect/ing the species distribution.

Eight felid species have been identified on the Iberian Peninsula, from small carnivores such as the wildcat (*Felis silvestris*), up to the middle-sized lynx (*Lynx pardinus, Lynx lynx* and *Lynx spelaea*), and big carnivores such as the leopard (*Panthera pardus*) and several species of lion (*Panthera leo clueti, Panthera spelaea* and *Panthera* sp.). A diachronic and biogeographic analysis of this carnivore family allows a better comprehension of mammal adaptations to changing environments.

Biogeographische Analyse von oberpleistozänen Feliden (*Felis*, *Lynx* und *Panthera*) Überresten in archäologischen Stätten auf der Iberischen Halbinsel

Dieses Papier gibt eine Einführung in die biogeographische Verteilung von Feliden (*Felis*, Luchs und *Panthera*). Der analysierte Zeitraum liegt innerhalb der letzten Vereisungsphasen. Dieser Zeitraum war recht instabil, da sich die wechselnden klimatischen Bedingungen auf die biogeographische Verteilung der Säugetiere auswirkten. Ich konzentriere mich bei dieser Analyse auf die Iberische Halbinsel, die südwestlichste Region Europas. Es handelt sich jedoch um eine komplexe Geographie mit unterschiedlichen klimatischen Gebieten, die sich auf die Verbreitung der Arten auswirken. Auf der Iberischen Halbinsel wurden acht Felidarten identifiziert, von kleinen Fleischfressern wie der Wildkatze (*Felis silvestris*) bis hin zum mittelgroßen Luchs (*Lynx pardinus*, *Lynx lynx* und *Lynx spelaea*) und großen Fleischfressern wie dem Leoparden (*Panthera pardus*) und mehrere Löwenarten (*Panthera leo clueti*, *Panthera spelaea* und *Panthera* sp.). Eine diachrone und biogeographische Analyse dieser Fleischfresserfamilie ermöglicht ein besseres Verständnis der Anpassungen der Säugetiere an Umweltveränderungen.

no.	site	location	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.
1	Cueva Eirós	Triacastela, Lugo						×			
2	Las Caldas	Priorio, Asturias						×			
3	La Güelga	Cangas de Onís, Asturias						×			
4	La Riera	Posada de Llanes, Asturias						×	×	×	
5	Llonín	Peñamera Alta, Asturias						×			
6	La Paloma	Soto de Regueras, Asturias	×						×		
7	Colombres	Ribadeva, Asturias	×								
8	Cueto de la Mina	Llanes, Asturias	×								
9	Tudela Veguín	Grado, Asturias	×								
10	Sima del Sueve	El Sueve, Asturias				×					
11	Tito Bustillo	Ribadesella, Asturias			×						
12	Balmorí	Llanes, Asturias									×
13	Quintanal	Llanes, Asturias									×
14	La Parte	Siero, Asturias								×	
15	Hornos de la Peña	S. F. de Buelna, Cantabria				×		×			
16	Castillo	Puente Viesgo, Cantabria						×	×	×	
17	El Juyo	Igollo, Cantabria						×			×
18	Morín	Villaescusa, Cantabria	×		×	×		×			
19	El Mirón	Ramales, Cantabria	×								×
20	El Otero	Voto, Cantabria	×								
21	Covalejos	Arce, Cantabria	×								
22	Valle	Ramales, Cantabria	×								

Tab. 1 Archaeological sites at the Cantabrian Corniche, location of the sites and felid species presence.

no.	site	location	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.
23	Rascaño	Miera, Cantabria				×					
24	Altamira	Santillana del Mar, Cantabria				×	×		×		
25	Cueva San Juan	Arredondo, Cantabria						×			
26	El Pendo	Camargo, Cantabria							×		×
27	Covacho Arenillas	Islares, Cantabria						×			
28	El Cuco	Castro Urdiales, Cantabria						×			
29	Las Pajucas	Lanestosa, Bizkaia				×		×			
30	Arlanpe	Lemoa, Bizkaia						×			×
31	Atxuri	Mañaria, Bizkaia						×			
32	Oyalkoba	Abadiano, Bizkaia						×			
33	Bolinkoba	Abadiano, Bizkaia		×				×			
34	Axlor	Dima, Bizkaia				×		×			
35	Goikolau	Mañaria, Bizkaia	×								
36	Lumentxa	Lekeitio, Bizkaia	×			×	×				
37	Santimamiñe	Kortezubi, Bizkaia	×			×			×		
38	Lamiñak II	Berriatua, Bizkaia	×								
39	Urratxa III	Gorbea, Bizkaia				×					
40	Venta Laperra	Carranza, Bizkaia		×							
41	El Polvorín	Carranza, Bizkaia		×							
42	Arrillor	Zigoitia, Araba	×	×		×					
43	Peñas de Oro	Zuia, Araba	×								
44	Praileaitz I	Deba, Gipuzkoa						×			
45	Astigarraga	Deba, Gipuzkoa	×			×		×			
46	Ekain	Deba, Gipuzkoa						×			

Tab. 1 (continued)

no.	site	location	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.
47	Amalda	Zestoa, Gipuzkoa		×	×			×	×	×	
48	Lezetxiki	Arrasate, Gipuzkoa	×	×		×		×		×	
49	Labeko Koba	Arrasate, Gipuzkoa	×								
50	Aitzbitarte III	Errenteria, Gipuzkoa						×			
51	Marizulo	Urnieta, Gipuzkoa	×								
52	Urtiaga	Deba, Gipuzkoa	×	×		×			×	×	
53	Ermittia	Deba, Gipuzkoa		×							
54	Aitzbitarte IV	Errenteria, Gipuzkoa								×	
55	Abauntz	Arraitz, Navarra	×					×	×		
56	Coscobilo	Olazagutia, Navarra						×			
57	Zatoya	Abaurrea Alta, Navarra		×							

Tab. 1 (continued)

no.	site	location	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.
58	Prado Vargas	Cornejo, Burgos						×			
59	Valdegoba	Huérmeces, Burgos	×	×	×			×			×
60	Cueva de la Ermita	Hortigüela, Burgos						×			
61	Caballón	Oña, Burgos	×	×			×	×			
62	La Blanca	Oña, Burgos	×	×							
63	Cueva Millán	Hortigüela, Burgos	×		×						
64	Cueva de Aguilón	Aguilón, Zaragoza						×			
65	Zarzamora-Buho	Perogordo, Segovia						×			
66	Camino	Pinilla del Valle, Madrid						×			
67	Cueva de los Torrejones	Tamajón, Guadalajara						×			

Tab. 2 Archaeological sites at the centre of the Iberian Peninsula and southern side of the Pyrenees, location of the sites and felid species presence.

no.	site	location	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.
68	Cueva de los Casares	Riba de Saelices, Guadalajara	×	×	×		×	×			×
69	Moros de Gabasa	Peralta de Calasanz, Huesca	×		×	×		×			×
70	Cova dels Muricecs	Llimiana, Lleida		×	×			×			
71	Estebanvela	Ayllón, Segovia	×	×							
72	Congosto	S. Andrés del Congosto, Guadalajara	×		×		×				
73	Chaves	Casbas de Huesca, Huesca		×							
74	Gato II	Épila, Zaragoza		×							
75	Jarama VI	Valle del Jarama, Guadalajara									×

Tab. 2 (continued)

no.	site	location	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.
76	Cova de S'Espasa	Oix-Sardenes, Girona						×			
77	Cova dels Ermitons	Sales de Llierca, Girona			×			×			
78	Cova de l'Arbreda	Serinyá, Girona	×	×	×	×		×			×
79	Bora Gran	Serinyá, Girona	×				×				
80	Mollet I	Serinyá, Girona			×	×		×			×
81	Mollet III	Serinyá, Girona			×						
82	Reclau Viver	Serinyá, Girona			×						×
83	Olopte	Isobol, Girona			×	×					
84	Cau del Duc	Torroella de Montgrí, Girona		×	×	×		×			
85	Abric Romaní	Capellades, Barcelona	×	×				×			

Tab. 3 Archaeological sites at the Mediterranean coast, location of the sites and felid species presence.

no.	site	location	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.
86	Cova del Gegant	Sitges, Barcelona		×	×			×			
87	Cau de Coçes	Sitges, Barcelona		×							
88	Musclé	Sitges, Barcelona		×	×						
89	Castell-defels	Castell-defels, Barcelona	×					×			
90	Toixoneres	Toixoneres, Barcelona	×		×						
91	Toll	Moiá, Barcelona	×	×	×	×					×
92	Cingle Vermell	Vilanova de Sau, Barcelona					×				
93	Parco	Alos de Llobregat, Barcelona					×				
94	Cova Foradada	Calafell, Tarragona						×			
95	Cova de L'Olla	Marmellar, Tarragona		×		×					
96	Balma de la Griega	Calafell, Tarragona					×				
97	Matutano	Vilafamés, castellón	×	×			×				
98	Cueva Horadada	Azuebar, Castellón						×			
99	Cueva de les Meravelles	Alzira, Valencia						×			
100	Bolomor	Tavernes de Valldigna, Valencia						×			×
101	Mallaetes	Barx, Valencia					×	×			
102	Cova Negra	Xátiva, Valencia	×	×				×			×
103	Cova de Racò del Duc I	Vilallonga, Valencia						×			
104	Parpalló	Gandía, Valencia	×				×				
105	Abrigo de la Quebrada	Chelva, Valencia					×				
106	Cova del Corb	Ondara, Alicante				×		×			

Tab. 3 (continued)

no.	site	location	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.
107	Cova Foradada	Xàbia, Alicante						×			
108	Cova de les Calaveres	Benidoleig, Alicante						×			
109	Cova del Parat	Tollos, Alicante						×			
110	Cova del Salt	Alcoi, Alicante						×			
111	Abric del Pastor	Alcoi, Alicante						×			
112	Cendres	Teulada-Moraira, Alicante	×				×				
113	Beneito	Muro de Alcoy, Alicante	×				×				
114	Sima de las Palomas	Torre Pacheco, Murcia						×			
115	Cueva del Niño	Ayna, Albacete					×				
116	Cueva Negra	Caravaca de la Cruz, Murcia		×							

Tab. 3 (continued)

no.	site	location	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.
117	Cueva Ambrosio	Vélez Blanco, Almería	×	×			×				
118	Cueva de la Carigüela	Darro, Granada					×	×			
119	Cueva Horá	Darro, Granada		×							
120	Campana de Piñar	Piñar, Granada						×			
121	Cueva de Nerja	Nerja, Málaga	×	×			×				
122	Boquete de la Zafarraya	Alcaucín, Malaga		×				×			
123	Devil's Tower	Gibraltar		×				×			
124	Genista Cave	Gibraltar		×				×			
125	Vanguard Cave	Gibraltar						×			

Tab. 4 Archaeological sites at the southern and western sides of the Iberian Peninsula, location of the sites and felid species presence.

no.	site	location	*Felis silvestris*	*Lynx pardina*	*Lynx spelaea*	*Lynx lynx*	*Lynx* sp.	*Panthera pardus*	*Panthera leo*	*Panthera spelaea*	*Panthera leo* sp.
126	Gorham's Cave	Gibraltar	×				×	×			
127	Gruta do Escoural	Montemor-o-Novo	×		×			×			×
128	Gruta da Figueira Brava	Brava, Setubal	×					×			×
129	Pego do Diabo	Loures	×		×			×			
130	Pedreira da Salemas	Loures	×		×			×			×
131	Salemas	Peniche	×		×						
132	Gruta das Fontaìnhas	Cadaval	×					×			
133	Furninha	Peniche	×		×			×			
134	Casa da Moura	Óbidos						×			
135	Gruta da Oliveira	Torres Novas						×			
136	Gruta do Caldeirao	Tomar	×		×			×			
137	Lorga do Dine	Vinhais						×			×
138	Lapa da Rainha	Leira	×		×						
139	Columbeira	Bombarral	×		×						
140	Casa da Moira	Peniche		×							
141	Algar do Joao Ramos	Peniche		×	×						
142	Algar do Cascais	Lisboa			×						
143	Maltravieso	Cáceres, Extremadura		×							

Tab. 4 (continued)