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# New insights into the Middle Pleistocene paleoecology and paleoenvironment of the Northern Iberian Peninsula (Punta Lucero Quarry site, Biscay): A combined approach using mammalian stable isotope analysis and trophic resource availability modeling

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ABSTRACT

The northern coastal area of the Iberian Peninsula shows an excellent archaeo-paleontological record with a unique representation of Pleistocene mammalian fossils. While the Late Pleistocene is better recorded, the Middle Pleistocene record remains more fragmentary. The Punta Lucero site (Biscay) has yielded the most important fossil assemblage of the middle Middle Pleistocene for the northern Iberian Peninsula in both, number of identified specimens and taxonomic diversity. Punta Lucero constitutes a unique opportunity to evaluate Middle Pleistocene mammalian resource and habitat use, and trophic dynamics employing a combined approach: biogeochemical analysis and mathematical modeling. Stable isotope analysis points to resource partitioning between Punta Lucero cervids and bovids. Stable isotope analysis and trophic modeling evidence resource overlap and interspecific competition among predators, especially between the scimitar-toothed cat *Homotherium latidens* and the European jaguar *Panthera gombaszoegensis*. The trophic resource availability modeling assumes that *Canis mosbachensis* consumed a 20% of preys of more than 10 kg, mainly as carrion. Thus, while there would be a taxonomic overlap with those preys consumed by the large felids, the different strategy would have facilitated the coexistence of these canids with larger carnivores. Trophic modeling indicates a high competition among the predator guild. The potential presence of hominins in the area would have reached to an unsustainable situation. However, the potential presence of other prey species, such as *Equus* sp., would have made the ecosystem more sustainable. The methodology followed in this study highlights the potential of multidisciplinary approaches in the assessment of Pleistocene faunal dynamics.



## 1. Introduction

The Iberian Peninsula is the largest of the three southern European peninsulas and has played a key role in the Pleistocene regarding human evolution and as a refuge during glacial cycles (Muñoz-Sobrino et al., 2007; Álvarez-Lao and García, 2010; González-Sampériz et al., 2010; Arsuaga et al., 2014; Bérmudez de Castro et al., 2016). It combines a long coast (~4120 km) with a large part of the territory above 600 m.a.s.l. From an ecological and climatic point of view, it can also be further subdivided into two

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separate zones: most of the Iberian Peninsula has an overriding Mediterranean influence, while the northern fringe is under the influence of a Eurosiberian climate. These two zones are separated by the Cantabrian Mountain range, which, in certain aspects, constitutes a westwards continuation of the Pyrenees. During the late Pleistocene, it acted as a true ecogeographic barrier for certain macromammal species (Álvarez-Lao and García, 2010; Gómez-Olivencia et al., 2014). Pollen analyses and phylogeographic models pointed to the existence of a mosaic-like landscape of forests, woodlands, savannahs and steppes in the Iberian Peninsula even during the harshest climatic episodes of the Pleistocene (Carrión et al., 2010, 2012; Rodríguez-Sánchez et al., 2010; González-Sampériz et al., 2010). This patched landscape may have supported a high diversity of Quaternary fauna within refuge areas (Provan and Bennett, 2008; Álvarez-Lao and García, 2010; Finlayson et al., 2011). Particularly, the northern coastal area of the Iberian Peninsula experienced relatively mild conditions over the Pleistocene, thus constituting a key refuge area for a wide suite of temperate flora and fauna (Muñoz-Sobrino et al., 2007; Álvarez-Lao and García, 2010; González-Sampériz et al., 2010).

The Middle Pleistocene is a key period to understand the evolution of Western Europe ecosystems, and the distribution of human populations that occupied this area. The transition between the Early to the Middle Pleistocene was characterized by a shift in the astronomical forcing from a climate spectrum dominated by the low-amplitude 41 ka obliquity band to the high-amplitude 100 ka eccentricity band that has been operating for the last 800 ka. This change brought about a significant increase in the volume of global ice and determined the current glacial-interglacial dynamics (Zachos et al., 2001; Lisiecki and Raymo, 2005). The beginning of the Middle Pleistocene is also marked by the Villafranchian-Galerian faunal turnover (~1.0–0.9 Ma; Kahlke et al., 2011; Belluci et al., 2015), and the so called Mid-Pleistocene Revolution (MPR) (Maslin and Ridgwell, 2005). With this faunal turnover, new carnivores appeared in Europe and herbivore diversity increased progressively (e.g. Turner, 1992; Azanza et al., 2004; Rodríguez et al., 2004; Cuenca-Bescós et al., 2005; Meloro et al., 2007; Palombo, 2007; Raia et al., 2007; Meloro, 2011). During the Middle Pleistocene, paramount events regarding human evolution were recorded in the Iberian archaeo-paleontological record. The beginning of the Middle Pleistocene witnessed the demise of hominins that used Mode 1 technology and who inhabited Europe during the late Early Pleistocene (*Homo antecessor*; Bermúdez de Castro et al., 2016). The middle Middle Pleistocene recorded the arrival of new populations (c. 600–500 ka BP) with Mode 2 technology (Bermúdez de Castro et al., 2016 and references therein) and the emergence of the first populations with clear Neandertal affinities c.430 ka BP (Sima de los Huesos, Sierra de Atapuerca; Arsuaga et al., 2014).

Due to the abundance of shelters and caves formed on its vast karstic landscapes, the northern fringe of the Iberian Peninsula preserves an excellent archaeo-paleontological record of MIS 3 and 2 (e.g., Altuna, 1972; Castaños, 2005; Álvarez-Lao, 2014; Domingo et al., 2005–2006), including renowned (and increasing; e.g., Garate Maidagan and Rivero Vilá, 2015) evidence of prehistoric human art. However, the Middle Pleistocene record is sparse and fragmentary in the northern fringe of the Iberian Peninsula and thus, archaeo-paleontological localities of this chronology are of great relevance to gain insights about the paleoclimatic, paleoenvironmental and paleoecological shifts that took place during this time period in the region. In the last years, the re-assessment of three paleontological sites (Llantrales, Mestas de Con, Punta Lucero), the description of new sites (La Parte, Santa Isabel de Ranero) and new chronological studies are providing new insights about the Iberian Middle Pleistocene in the Cantabrian region (Torres et al., 2001, 2014; Álvarez-Lao and García-García, 2006; Gómez-Olivencia et al., 2015; Álvarez-Lao, 2016). However, little is known regarding the paleoecology of the macro-mammal communities that inhabited this area in this time period. Despite their relative good record in other parts of the Iberian Peninsula, only three sites could be located in the middle Middle Pleistocene (i.e., ca 400–600 ka BP) of the Northern fringe of Iberia: Llantrales, Mestas de Con and Punta Lucero (see text below; Fig. 1, Table 1). Other Middle Pleistocene sites (or sites that could be attributed to this chronology based on typological criteria of the lithics) from this region are more recent, lack a proper chronostratigraphical context, and/or have not yielded macro-mammal remains (e.g., Santa Isabel de Ranero: Torres et al., 2001, 2014; Irikaitz: Arrizabalaga and Iriarte, 2005; Lezetxiki: Falguères et al., 2005–2006; Goikoetxe: Edeso et al., 2011; Arlanpe, Ondiz: Rios-Garaizar et al., 2012, 2013, 2015; among others).

In this regard, paleoenvironmental and paleoecological data can be obtained from different proxies, such as stable isotope analysis (e.g., Domingo et al., 2012, 2013, 2015; García et al., 2015), and trophic resource availability modeling (e.g., Bermúdez de Castro et al., 1995; Fariña, 1996; Palmqvist et al., 2003; Vizcaíno et al., 2004, 2010; Rodríguez et al., 2014; Rodríguez-Gómez, 2015; Rodríguez-Gómez et al., 2013, 2014, 2016a, 2017a, b). Stable isotope analyses on Quaternary terrestrial mammalian taxa constitute an excellent proxy to obtain high-resolution paleoclimatic and paleoenvironmental terrestrial trends (e.g., Stevens and Hedges, 2004; Tütken et al., 2007; Fox-Dobbs et al., 2008; Stevens et al., 2008; Drucker et al., 2011; Domingo et al., 2015), and information on resource and habitat use and trophic dynamics (Bocherens and Drucker, 2003; Coltrain et al., 2004; Fox-Dobbs et al., 2007, 2008; Tütken et al., 2007; Prevosti and Martin, 2013; Domingo et al., 2015). This line of research, focused on the investigation of the recent past of the Earth's history, is crucial to understand the response of faunal communities in a scenario of changing climate and persistent human pressure that is pushing ecosystems to more unstable conditions.

Trophic resource availability modeling is providing new insights into the Early and Middle Pleistocene paleoecology. This line of research is based on modeling palaeocommunity trophic relationships in order to estimate resource availability, which allows testing different hypotheses regarding the resource use of ancient species. At the moment, this model has been applied to a local scale to study the large mammal paleocommunities from the Sierra de Atapuerca (Rodríguez-Gómez et al., 2013, 2014, 2017a) and the Orce sites (Rodríguez-Gómez et al., 2016a, 2017b) in Spain; and at continental scale, in European sites (Rodríguez-Gómez, 2015; Rodríguez-Gómez et al., 2017c). These studies have provided relevant information of first European setters, among other aspects: rejecting cannibalism at Gran Dolina-TD6 as the result of long-term scarcity of resources (Rodríguez-Gómez et al., 2013); supporting the human absence at the Sierra de Atapuerca 600.000 years ago due to an increased resource competition between secondary consumers (Rodríguez-Gómez et al., 2014); appointing that the taphocenose in Gran Dolina-TD6 is incomplete and suggesting that this paleocommunity paleocommunity likely included a large felid species not recorded in the fossil assemblage (Rodríguez-Gómez et al., 2017a); showing that the large mammal assemblage with the first human population in Western Europe, represented by two Orce sites from Spain, Barranco León-D and Fuente Nueva-3 (Toro-Moyano et al., 2013), were not limited by the meat resource availability (Rodríguez-Gómez et al., 2017a); suggesting that the human settlement in Orce was probably not a matter of ecological opportunity because competition intensity in the carnivore guild of Venta Micena, site older than Barranco León-D and Fuente Nueva-3, was lower than in them, (Rodríguez-Gómez et al., 2017b); supporting a