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Brown bear (*Ursus arctos* L.) palaeoecology and diet in the Late Pleistocene and Holocene of the NW of the Iberian Peninsula: A study on stable isotopes

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ABSTRACT

In this paper we performed stable isotope analysis on bone collagen of 81 samples from at least 39 brown bears (*Ursus arctos*) dating from Late Pleistocene to nowadays, that lived in the western of the Cantabrian Mountains. To interpret the data obtained we compared brown bear stable isotope signatures with those of cave bears (*Ursus spelaeus*), red deer (*Cervus elaphus*), and humans (*Homo sapiens*) from the same area. We observed that the diet of cave bears and brown bears in the Cantabrian Mountains was based on vegetable matter, although their different isotopic signatures suggest different ecological niches: wooded lowlands for the cave bear and steep highlands with scarce tree cover for the brown bear. In the Holocene brown bear maintains isotopic signatures similar to the Pleistocene ones in spite of the climatic tempering, which seems to be related to an even greater displacement toward the uplands due to a greater anthropic pressure in the ecosystem.

1. Introduction

1.1. The brown bear in the Iberian Peninsula

The brown bear (*Ursus arctos* LINNAEUS 1758) is a common species in the Holocene fauna of the Iberian Peninsula that in historical times underwent a significant reduction in its distribution and population size by the increasing human pressure (Palomero et al., 2007). In addition, although less abundant, it is also found in Pleistocene deposits of the Cantabrian mountain range, sharing space and perhaps habitat with the most abundant (judging by the number of recovered remains) cave bear (García-Vázquez et al., 2015). An interesting question to better understand the ecology of this species is to know its diet and its relation to other large mammals in the past, and to determine its ecological niche evolution along time from before the last glacial maximum (LGM) to its current situation.

When attempting to reconstruct the ecology of an extinct animal, it is usual to resort to morphofunctional studies and comparison with closely related current species. Here we study the diet of the End-Pleistocene and Holocene brown bear from the Northwest of the Iberian Peninsula. What may seem simple, since the brown bear has present representatives even in the same areas as in the past, is not so much if we consider that the ecosystems of the late Pleistocene and even the early Holocene differ from the present in many aspects. The climate during MIS 3, even though it was an interglacial episode, was generally colder than the Holocene climate although subjected to millennial scale climatic fluctuations (Fletcher et al., 2010), and vegetation reflects these fluctuations, as shown by pollen studies on continental or marine deposits (Naughton et al., 2007; Jalut et al., 2010). Post-glacial climatic moderation significantly modified ecosystems (Fletcher et al., 2010; Huntley et al., 2013), although the Holocene is not a homogeneous period as there were both global climate events (such as a global cold pulsation 8200 years BP) and small variations in local conditions, depending on latitude, altitude, topography or distance from the sea (Railsback et al., 2011; Domingo et al., 2015).

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1.2. Palaeoecology and stable isotope analysis

An approach to the diet of extinct animals is the study of stable isotopes of C and N, in this case in collagen preserved in bone tissue. Thanks to the relative stability of bone collagen over time, stable isotope analysis (SIA) may allow a reconstruction of the brown bear diet as was already done for other ursids, such as the extinct cave bear (*Ursus spelaeus* ROSENMÜLLER 1794), for which SIA demonstrated a predominantly herbivorous diet throughout Europe (e. g. Bocherens et al., 1994, 1997, 1999; Nelson et al., 1998; Fernández-Mosquera et al., 2001; Vila Taboada et al., 2001; Krajcarz et al., 2016; Naito et al., 2016) as was shown by morphological studies of the skull and jaw (Grandal-d'Anglade, 2010; van Heteren et al., 2014, 2016). Although in some localized cases the isotopic values are anomalous (Richards et al., 2008; Robu et al., 2013) they do not correspond to a carnivorous diet, but are likely to respond to particular ecological circumstances (Bocherens et al., 2014a; Bocherens, 2015).

The basis of SIA is relatively simple: both carbon and nitrogen occur in nature in two major isotopes, one lighter and one heavier. At natural abundance, the light isotope is the most abundant. The ratio between light and heavy isotope in a given tissue reflects the type of nutrients assimilated by the individual, since each large group of food items (C3 or C4 plants, leguminous plants, herbivorous animals, oceanic or freshwater fish …) have characteristic isotopic proportions (Van Der Merwe, 1982; Schoeninger and DeNiro, 1984; Peterson and Fry, 1987; Koch, 1998; Drucker et al., 2008) and these differences occurring at the baseline of the food chain are transmitted throughout the network with a specific variation (isotopic fractionation) at each trophic level.

Isotopic studies conducted for the determination of the diet of fossil organisms are performed usually on the collagen preserved in the bones. Collagen is the protein that confers elasticity and resistance to bone tissue. Being a protein, it will record the isotopic values derived from the proteins that the individual was fed with the corresponding factor of variation (fractionation) that occurs during the assimilation of the proteins and the collagen synthesis itself. In large mammals, the average renewal rate of bone collagen is about 10 years (Tykot, 2003), so its isotopic study allows reconstructing the individual's diet for a long period of life.

Throughout the Holocene, the evolution of ecosystems after deglaciation would also have an influence on the brown bear isotopic signature. This evolution is manifested in a change in the predominant type of vegetation and also in the composition of the faunal communities. The increase of woods with deciduous species (Fletcher et al., 2010) and the extirpation of large, cold-adapted herbivores (Álvarez-Lao and García, 2010) are important features that differentiate the Pleistocene from the Holocene in the Iberian Peninsula.

1.3. Brown bear physiology and diet

The brown bear in the present is a species with a great plasticity in its eating habits. Its diet includes plants, mushrooms, honey, insects (ants, bees and wasps), oligochaetes, micromammals, ungulates and fish, especially anandromous salmonids, and even soil (geophagy) or bone (osteophagy) (Couturier, 1954; Clevenger, 1991; Parde and Camarra, 1992; Mattson, 1997, 2001, 2002; Hilderbrand et al., 1999a, 1999b, Mattson et al., 1999, 2002a, 2002b; Nomura and Higashi, 2000; Gende et al., 2001; Wald, 2011), but its eating habits depend on the availability of food and its energy requirements (Welch et al., 1997; Rode and Robbins, 2000).

In the months prior to hibernation, the bear exhibits high appetite and high nutrient intakes (hyperphagia) to accumulate fat storages (Welch et al., 1997). Hibernation is a period of variable duration during which the bear does not eat water or food, nor urinate or defecate. However, its metabolism does not slow down substantially (Hissa, 1997). The bear gets its energy from stored fats, and muscle mass is not lost, but renewed (Lohuis et al., 2007). The products of catabolism, such as urea, are not excreted but recycled (Nelson et al., 1975; Floyd et al., 1990; Barboza et al., 1997) and the bone tissue does not suffer losses but is actively remodelling (Donahue et al., 2006; Lennox and Goodship, 2008; McGee et al., 2008), although at a lower rate than during the active season. During hibernation the synthesis of proteins is made from the nitrogen compounds produced thanks to the recycling of the reabsorbed urea. Recycling involves the synthesis of amino acids from carbonate skeletons and amino groups that have already undergone previous isotopic fractionation, so an alteration in the nitrogen isotope signal in bears with respect to other animals with the same diet would be expected. Studies in cave bears suggest that the effect of hibernation on the isotopic values of bone collagen is only reflected in bears from colder periods, with longer hibernation (Grandal-d'Anglade and Fernández Mosquera, 2008). Accordingly, a rise in the isotopic values of nitrogen was observed in cave bears towards the end of the MIS 3 (Fernández-Mosquera et al., 2001; Pérez-Rama et al., 2011a), although the cause of this evolution of isotope signatures can also be environmental variations related to the cooling climate that affected the isotopic values from the bottom of the food chain, either globally or locally (Drucker et al., 2003; Bocherens et al., 2014b).

Studies on the diet of present Cantabrian and Pyrenean brown bears are mainly based on fecal analysis (Couturier, 1954; Clevenger, 1991; Braña et al., 1993; Naves et al., 2006), although it should be noted that this approach underestimates the proportion of meat in the diet (Robbins et al., 2004). From all these studies it can be concluded that the diet of Iberian brown bears is characterized by the sequential selection of food throughout the seasons, with vegetables being the major part of their diet (Rodríguez et al., 2007). In the Cantabrian mountain range, grasses are the most frequently food in spring, but the bears also consume carrion if available. In the summer the preferred food are fleshy fruits, and in autumn and early winter the nuts. In general, acorns and blueberries are the basic foods for the brown bear in the region (Naves et al., 2006). Summer is the season in which food of animal origin is most important, although the intake of insects is, by volume, almost double than that of mammals (Braña et al., 1993). The Cantabrian brown bear does not behave as an active hunter, but as an opportunistic scavenger. Animal protein is less than 20% of the present Cantabrian bears diet (Clevenger, 1991; Braña et al., 1993; Naves et al., 2006), whereas in the Pyrenean bears it reach about 30% (Couturier, 1954). A difference between the two populations is that Pyrenean bears incorporate more tubers (such as pignut, *Conopodium majus* (GOUAN) LORET 1886) and roots into their diet, and they also feed, albeit occasionally, aquatic animals such as frog and trout (Couturier, 1954).

1.4. Objectives

One might think that the diet of the brown bears fossils studied in this work was simply the same as the bears that today occupy the Cantabrian Mountains. However, climatic changes throughout the Pleistocene could have caused differences in the diet of the bear, as today it differs between brown bears from the North and those from the South of Europe, being more carnivores the first (Vulla et al., 2009). It is also possible that the anthropogenic influence in the ecosystem will cause habits and diets to differ. In contrast to the cave bear, isotopic studies on fossil brown bear are relatively scarce (Bocherens et al., 2004, 2011; Münzel et al., 2011) and none have been carried out until now for the Iberian brown bear. The

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