



Rabbit exploitation in the Middle Paleolithic at Gruta Nova da Columbeira, Portugal

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ABSTRACT

Subsistence differences between Neanderthals and anatomically modern humans may suggest key behavioral changes during the Middle to Upper Paleolithic transition. In this paper, we present zooarchaeological and stable isotopic analyses of *Oryctolagus cuniculus* (European wild rabbit) remains from levels 6, 7, 8 and 9 in addition to new dates of Gruta Nova da Columbeira, a Mousterian cave site located in central Portugal. We use these data to explore two alternative hypotheses: 1. Anatomically modern humans gained a competitive advantage over Neanderthals by exploiting a broader-spectrum diet including small prey items such as the rabbit and 2. Neanderthals already on occasion practiced a broad spectrum diet in at least some locations. Using an interdisciplinary approach to the study of an older collection, this study suggests Neanderthals incorporated *Oryctolagus* as a small component of their diet at Gruta Nova de Columbeira.

1. Introduction

How did anatomically modern humans (AMH) and late Neanderthals exploit their environments and adapt to environmental changes during the Upper Pleistocene? This question is not only relevant to research on current human adaptation to global climate change, but is essential for understanding Neanderthal extinction and replacement by AMHs. Two models have been influential for understanding the disappearance of Neanderthals in Europe: 1.) the recent out-of-Africa or replacement model, which proposes that AMHs migrated from Africa into Europe and Asia and replaced archaic populations in those continents due to some selective advantage (e.g., Stringer and Andrews, 1988; Mellars, 1996; Klein, 2008); and 2.) the multi-regional model, which posits that Neanderthals and AMHs interacted genetically, contributing to subsequent populations of Europe through gene flow, and that the disappearance of Neanderthals occurred through genetic mixing and swamping instead of direct competition between two species (Thorne and Wolpoff, 1981; Clark and Lindley, 1989; Wolpoff, 1999; Clark, 1999, 2002). Questions of how AMHs spread through Europe (Bon, 2002; Rigaud, 1997; Bordes, 2006; Hublin, 2007; Davies, 2007), the extent to which Neanderthals and AMHs interacted during Middle to Upper Paleolithic transition (~40–30 kaBP) (Bordes, 2003; Floss, 2003; Smith et al., 2005; Zilhão, 2013; Higham et al., 2010, 2014), and how processes such as

competition, gene flow, and population replacement worked together to result in the Upper Paleolithic landscape in Europe (Wolpoff and Caspari, 1997; Bräuer and Stringer, 1997) have all been explored as part of this larger debate. More recently, detailed studies focusing on Neanderthal DNA encountered in modern human genetics seem to reinforce the idea of gene flow between these populations (Sankararaman et al., 2014; Vernot and Akey, 2014).

Comparison of AMH and Neanderthal subsistence strategies is one way in which these models have been evaluated. For decades, the Upper Paleolithic of Europe was often viewed as the origin of modern hunter gatherer behavior (Gamble, 1986; Chase, 1986; Binford, 1989; Marks, 1989; Stiner, 1991; Bar-Yosef, 1994; Soffer, 1994); the onset of exploitation of small prey items such as tortoises, leporids, and birds (Stiner et al., 1999, 2000), and the exploitation of dangerous animals such as bison and mammoth is one commonly-cited component of such behavior (Klein, 1989) although this view of modernity is argued by some to be outdated (McBrearty and Brooks, 2000; Henshilwood et al., 2003; Marean, 2007). Foraging strategies that include both large and dangerous game, as well as sessile or slow small game, may suggest behaviors such as cooperation and the creation of special technologies like nets or traps (Stiner et al., 2000; Stiner, 2001). The increase in diet breadth of Upper Paleolithic hominins may therefore reflect an adaptation of AMH foraging strategies to larger populations (e.g., Stiner et al., 2000). In this argument, AMH foragers sought lower ranked prey

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items such as tortoises, hares, and mollusks, and correspondingly developed technology to more efficiently exploit these resources in response to population pressure. However, some (e.g., Hockett and Bicho, 2000; Hockett and Haws, 2002; Jones, 2006, 2016; Dean, 2007; Driver and Woiderski, 2008) have noted that the evidence for the Upper Paleolithic does not perfectly fit this scenario. In addition, evidence of Neanderthal exploitation of small prey has been identified in Europe and the Levant (Laroulandie, 2004, 2005; Sanchis Serra and Fernandez Peris, 2008; Blasco and Fernández Peris, 2009; Blasco et al., 2010; Brown et al., 2011; Hardy and Moncel, 2011; Henry et al., 2011; Blasco and Peris, 2012; Cochard et al., 2012) and the amount of evidence continues to build, including in Portuguese Estremadura (Nabais, 2011).

The Middle to Upper Paleolithic transition did not occur uniformly across time and space, but was rather a mosaic of change (Straus, 2005). An exploration of regional subsistence differences between AMHs and Neanderthals is thus necessary. On the Iberian Peninsula, where Neanderthals may have survived until relatively recently (e.g., Zilhão et al., 2010, Haws et al., 2011; see Higham et al., 2014 for contesting argument), archaeologists have proposed several models of Neanderthal replacement by AMHs, but as with many aspects of the study of Neanderthal behavior and ecology, these models are contested. The Ebro Frontier hypothesis is one such model which posits that most of Iberia worked as a refugium in where Neanderthals survived for several thousands of years longer than in the rest of Europe (Zilhão, 1993, 2000, 2006; Zilhão et al., 2010; d'Errico and Goñi, 2003; Banks et al., 2008). However, problems with radiocarbon date accuracy, chronological modeling (Pettitt and Zilhão, 2015) and too few assays mean this model has never been conclusively tested (Wood et al., 2013).

Similarly, Neanderthal and AMH subsistence models in Europe require further testing. Scholars using subsistence information to understand the Middle to Upper Paleolithic transition in Iberia often turn to the study of the exploitation of the wild European rabbit (*Oryctolagus cuniculus*). Archaeofaunal assemblages from Iberian sites suggest Upper Paleolithic hominins regularly and systematically exploited rabbits as part of their diet (e.g., Aura et al., 2002; Sanchis Serra and Fernandez Peris, 2008; Hockett and Bicho, 2000; Hockett and Haws, 2002; Haws and Valente, 2006). Some models suggest the incorporation of the rabbit into the AMH diets was an adaptation to increasing population (e.g., Stiner, 2001); others suggest AMHs sought rabbits to fulfill specific nutritional purposes (Hockett and Haws, 2003). In either case, exploitation of the wild European rabbit may attest to an important shift in foraging adaptations: acquisition of small, fast-moving animals requires a different skillset than the pursuit of larger and/or slower prey types (Stiner et al., 1999, 2000). The exploitation of *Oryctolagus* may therefore provide insight into the practice of complex foraging behaviors as aspects of the overall adaptations of different hominin populations/subspecies.

While AMH exploitation of the European rabbit is well established, whether Neanderthals exploited this species is a matter of debate. Fa et al. (2013) argue that Neanderthals on the Iberian Peninsula ignored the abundant lagomorph species, giving AMHs a competitive advantage. However, recently analyzed faunal assemblages, notably that from Cueva del Bolomor (Blasco and Peris, 2012), suggest that at least some Neanderthals consumed a broad spectrum diet including smaller animals like rabbits, birds and tortoises. In this paper, we use the archaeofaunal *Oryctolagus* assemblage from Gruta Nova da Columbeira (Portuguese Estremadura) to explore behavioral differences and similarities in AMH and Neanderthal diet that may have contributed to the Neanderthal disappearance in Europe.

1.1. Small game exploitation and why it matters

Though we have an incomplete picture of the role small game played in the Neanderthal diet, both in Europe as a whole and on the

Iberian Peninsula in particular, this situation is beginning to change (Sanchis Serra and Fernandez Peris, 2008; Blasco et al., 2010; Blasco and Peris, 2012; Cochard et al., 2012). Recent evidence from a handful of Middle Paleolithic sites in Iberia and the southwestern France suggests Neanderthals occasionally adopted a broader spectrum diet that included small prey items (Blasco and Fernández Peris, 2009; Brown et al., 2011; Hardy and Moncel, 2011; Henry et al., 2011; Nabais, 2011). In Iberia as well as in the Levant and Italy, Neanderthals in at least some instances consumed tortoises (Stiner, 1994; Blasco, 2008; Nabais, 2011; Blasco et al., 2016). In France, Gibraltar, Croatia and Italy, Neanderthals exploited birds for both food and feathers, the latter possibly for ornamentation (Laroulandie, 2004, 2005; Peresani et al., 2011; Finlayson et al., 2012; Romandini et al., 2014; Radović et al., 2015; Fiore et al., 2016). And even the wild European rabbit, judged by many not to have been a component of the Neanderthal foraging strategy but present in archaeological sites due to in situ death or non-human carnivore activity (Fernández-Jalvo and Andrews, 2000; Sanchis, 2000; Stewart, 2004; Karavani and Patou-Mathis, 2009; Lloveras, 2010; Lloveras et al., 2011; Shipman, 2012; Fa et al., 2013), seems in at least some cases to have been exploited by Neanderthals. Six categories of evidence of anthropogenic accumulations of rabbit bones have been proposed (Martínez-Polanco et al., 2017): cut marks left behind by skinning, disarticulation and defleshing activities (Pérez-Ripoll, 1992; Cochard, 2004; Lloveras et al., 2009; Sanchis, 2010), the presence of rabbit long bone shaft cylinders, suggestive of intentional breakage for marrow extraction (Hockett, 1995; Cochard, 2004; Pérez Ripoll, 2004; Landt, 2007; Lloveras et al., 2009; Blasco and Peris, 2012; Cochard et al., 2012), human tooth marks on the bone surface (Cochard, 2004; Ibañez & Saladié, 2004; Pérez Ripoll, 2004; Landt, 2007; Lloveras et al., 2009) signs of thermal alteration such as burn marks on bone extremities or bone surface (Lloveras et al., 2009), high representations of biased age profiles towards adults (Cochard, 2004; Pérez Ripoll, 2004; Jones, 2006), and skeletal profiles with high incidences of mandibles, girdles, stylopodials and zeugopodials (Cochard, 2004; Pérez Ripoll, 2004; Yravedra, 2008; Lloveras et al., 2009). Excavations at Bolomor recovered rabbit remains bearing cut and burn marks of anthropogenic origin (Blasco and Peris, 2012; Blasco et al., 2010). Neanderthal consumption of leporids has also been recorded of the French Pyrenees at Les Canalettes (SE France; Cochard et al., 2012). In Gruta da Oliveira (Portuguese Estremadura) burned leporid remains are present across a number of Middle Paleolithic levels (Nabais, 2009). This apparent phenomenon of a broader diet practiced by Neanderthals has important implications for our understanding of Neanderthal subsistence practices and behavior.

The presence of small fauna in Middle Paleolithic deposits in and of itself, however, does not indicate broad spectrum hunting by Neanderthals. Archaeofaunal assemblages composed of small game may represent in situ death accumulations (e.g., Figueiredo, 2010; Pelletier et al., 2015). In addition, caves and rockshelters provide shelters or dens for a suite of species including cave bear (*Ursus spelaeus*), hyena (*Crocuta crocuta*), wolf (*Canis lupus*), cave lion (*Panthera leo spelea*), badger (*Meles meles*), red fox (*Vulpes vulpes*), lynx (*Lynx pardinus*), some raptorial birds, as well as hominins (e.g., Straus, 1982). Several of these same cave-occupying species have been known to prey upon leporids including predators such as wolf, pine marten (*Martes martes*), wildcat (*Felis silvestris*), golden eagle (*Aquila chrysaetos*), eagle owl (*Bubo bubo*), buzzard (*Buteo buteo*), and other species, as well as humans (Valverde, 1967; Delibes and Hiraldo, 1981; Angerbjörn and Flux, 1995; Cochard et al., 2012). Rigorous taphonomic studies are necessary to establish cases in which Neanderthals exploited a broad spectrum of prey types (Blasco and Peris, 2012; Blasco et al., 2010; Rodríguez-Hidalgo et al., 2013; Cochard et al., 2012; Lloveras et al., 2010, 2011, 2012).

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