

Continuity in animal resource diversity in the Late Pleistocene human diet of Central Portugal

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Abstract

Archaeologists studying the human occupation of Late Pleistocene Iberia have identified the Late Upper Palaeolithic, including the Pleistocene-Holocene transition, as a time of resource intensification, diversification and specialisation. The primary drivers for these changes were argued to be the result of population-resource imbalances triggered by the postglacial climatic warming and human population growth. Recent research, however, has pushed resource intensification and diversification back in time to the Early Upper Palaeolithic in Iberia and beyond. Dietary diversity may have given anatomically modern humans a selective advantage over Neanderthals. In this article we review the accumulated evidence for Late Middle and Upper Palaeolithic diet in central Portugal, emphasising the importance of small animal exploitation. We incorporate results from on-going research at Lapa do Picareiro and other sites to explore the possibility that the dietary choices of modern foragers in Iberia contributed to the extinction of the Neanderthal populations occupying the region until ca 30,000 ¹⁴C BP.

1 Introduction

Archaeologists studying the human occupation of Late Pleistocene Iberia often frame explanations for their subsistence economies within the now-classic 'Broad Spectrum Revolution' (BSR) model. Early work identified the Late Upper Palaeolithic, including the Pleistocene-Holocene transition, as a time of resource intensification, diversification and specialisation (Binford 1968; Clark 1987; Clark & Straus 1986; Clark & Yi 1983; Flannery 1969). The primary drivers for these changes were argued to be population-resource imbalances triggered by postglacial climatic warming and human population growth.

Recent research suggests that shifts in the types of small animals hunted may be correlated with population-resource dynamics across the Middle-Upper Palaeolithic transition in southern Europe (Stiner 2001; Stiner et al 1999; Stiner et al 2000). This new model replaced the simplistic, gradual model of diversification and intensification at the end of the

Pleistocene with one that linked situational shifts in different types of small game to human population pulses. Increased use of quicker, more reproductive animals (birds and rabbits) as slower, less reproductive types (shellfish, tortoises) declined in size and abundance suggested population pressure on the latter resources occurred earlier in the Palaeolithic. This model grounded the BSR concepts in an explicitly stated evolutionary ecological framework that tracked diet choice as a reflection of human demography.

In this article, we present an argument linking Palaeolithic human demography and diet choice from a nutritional ecology perspective (Hockett & Haws 2003, 2005). In Europe, small animal (and plant) utilisation appears to have begun in the Early Upper Palaeolithic with the arrival of anatomically modern *Homo sapiens* (AMHS). This adaptation may have enabled these foragers' populations to grow and

spread rapidly across landscapes that were sparsely populated by Neanderthals specialised in large game hunting. However, the late survival of Middle Palaeolithic Neanderthals in southern Iberia may have been due to a similar adaptation that kept AMHS out of an occupied ecological niche (Barton 2000; Finlayson et al 2008; Hockett & Haws 2005; Stringer et al 2008). Below we discuss the archaeological evidence for dietary behaviours in central Portugal and the implications for understanding long-term trends in Palaeolithic diets.

2 Conceptual background – demographic implications of dietary diversity

Archaeologists working on agricultural economies use the term *intensification* to mean an increase of labour input to extract higher yields from existing lands. In the case of hunter-gatherers, this can be accomplished either by increasing effort to extract more edible tissues from animal carcasses or by extracting additional animals or plants from a given unit of land. The latter may result in *specialisation* as greater time is allotted to the hunting or gathering of specific resources or in *diversification* if new resources previously ignored are exploited (usually defined by N-species rather than nutrient intake – see Hockett & Haws 2005:26, figure 2).

In the diet breadth model, *diversification* occurs once certain resources fall beneath an economic threshold for net caloric return, thus leading to the inclusion of new items. Technological innovations may also occur as part of these processes, such as the development of nets (Adovasio et al 1996). Both intensification and diversification are explicitly part of the diet breadth model, whereby increased effort for increasingly marginal returns would be considered a reduction in foraging efficiency. This in turn may be indicative of nutritional stress.

Most applications of the diet breadth model assume that large mammals (eg, ungulates) outrank smaller animals (eg, rabbits) in terms of post-encounter return rates (Broughton & O'Connell 1999), although notable exceptions to these resource ranking schemes have been identified (eg, Madsen & Kirkman 1988; Madsen et al 1997). As a result, the hunting of large game is interpreted as more efficient than the hunting of small game because optimisation models rank resources based on ratios of calorie output (energy expended) to calorie input (energy consumed).

Increasing focus on the hunting of small game such as rabbits and birds is generally interpreted as less energy efficient than the hunting of larger game. If behaviours that enhance energy efficiency are selected for, thereby driving mortality and fertility patterns, then the small game hunters and plant eaters should be at a selective disadvantage compared to those populations subsisting at a more energy-efficient level (eg, those eating primarily large game animals).

In the diet breadth model, population-resource imbalances lead to resource depression as higher-ranked resources decline. These imbalances are due to either overharvesting brought on by increased population or social pressures or by climate changes that alter habitats and reconfigure the spatial distribution of plants and animals. Causal mechanisms for population growth are assumed as the likely outcome of maximising energy through the focused hunting of so-called 'high-ranking' large game animals. This in turn would enhance selective fitness compared to diverse diets consisting of so-called 'low-ranking' small game animals and plant foods.

In contrast, Hockett and Haws (2003, 2005) and Hockett (2007) recently proposed an explanation for population growth based on nutritional ecology. By increasing dietary diversity and consuming a more balanced suite of essential nutrients, people would have had better overall health, higher reproductive rates and lower infant mortality rates that enabled population growth. Why should this occur? People may adopt strategies to minimise the risk of subsistence failures by targeting a diverse set of plant and animal resources (eg, Funk 2008) prior to, or independent of chronic nutritional stress. Given the climatic variability in the Late Pleistocene, this strategy may have been critical to survival and it may have been just this strategy that led to the success of AMHS and the ultimate demise of specific populations of archaic humans such as the European Neanderthals (Hockett & Haws 2005). Other factors, however, such as climatic changes that alter habitats and migrations of humans into already-occupied lands, are also recognised as factors that may change the set of resources available to human consumers, thereby forcing changes in human diet. Social dynamics, such as those Kuhn and Stiner (2006) outlined, emphasising the labour roles of AMHS, may have had significant impacts regarding diet choices as well. Women's collecting and small game hunting may have

provided a diverse diet and balanced essential nutrient intake thereby sparking positive changes in human demography.

Ultimately, the causal factors behind the demographic success of AMHS lie at the heart of the nutritional ecology approach. As defined in Hockett and Haws (2003), nutritional ecology focuses on the effects of essential nutrient intake (both calorie-providing macronutrients and the non-caloric vitamins and minerals) on human health, reproductive success and mortality. Nutritional ecology is a holistic approach to understanding the effects of dietary choice on the development and evolution of AMHS because it includes the full range of nutritional properties of food. The problem faced by the approach, as all models in the historic sciences ultimately must face, is operationalising the model. This includes, among other things, testing its assumptions against a poorly preserved archaeological record created by humans living in environments, and thinking about their social and ecological circumstances, in manners that have no modern analogues. When it comes to researching humans, uniformitarianism is not necessarily an absolute principle fully applicable in time and space (eg, Binford 2001). Nevertheless, it is quite plausible that AMHS in Europe had more diverse diets than Neanderthals given the available stable isotope, trace element and zooarchaeological record. While Palaeolithic diets arguably tended towards a diverse range of plants and animals (eg, Eaton et al 1997), Neanderthals in much of Europe became specialised large game hunters.

The following sections focus on the evidence for Late Middle and Upper Palaeolithic diets in Iberia. Our consideration of diversity emphasises the species richness in the published faunal assemblage data. Evidence for plant utilisation in our research area is precluded by preservation bias in the archaeological record. We find it plausible that human populations pursuing a diverse suite of small animals also actively collected a diverse set of plant resources (eg, Aranguren et al 2007). If that is the case, then small animal hunting may also serve as a proxy for diverse plant consumption – and this would be critical to an understanding of dietary influences on demographic patterns. We then expect that focused small animal exploitation should appear at the onset of the Upper Palaeolithic when modern populations colonised Iberia. In southern Iberia, the late survival

of Neanderthals may have resulted from a similar adaptation (Hockett & Haws 2003, 2005).

3 Late Pleistocene subsistence in Portugal

The Late Pleistocene archaeological record in southern and western Iberia offers a reasonably good dataset for studying long-term dietary trends. On the Iberian Peninsula, evidence for small animal utilisation, especially rabbits, is widespread during the Upper Palaeolithic but problematic for the Middle Palaeolithic.

Faunal preservation in open-air contexts is exceedingly rare but the Middle Palaeolithic site of Foz do Enxarrique (Brugal & Raposo 1999) offers a unique example. Middle Palaeolithic caves include the Galeria Pesada (Marks et al 2002), Oliveira (Zilhão 2000a,b; 2001), Caldeirão (Davis 2002), Figueira Brava (Antunes 2000a), and Gruta de Columbeira (Raposo 2000; Raposo & Cardoso 1998). Several caves and rockshelters in west-central Portugal provide important subsistence data for the Upper Palaeolithic, including Caldeirão (Davis 2002), Buraca Escura (Aubry et al 2001), Picareiro (Bicho et al 2000, 2006; Hockett & Bicho 2000; Haws 2003), Lagar Velho (Moreno-Garcia 2002), Anecrial (Almeida et al 2006), Lapa do Suão (Haws & Valente 2006), and Lapa dos Coelhoos (Hockett & Haws 2002). Tables 1 and 2 provide cumulative taxonomic and NISP data for the Late Middle and Upper Palaeolithic sites in central Portugal.

4 Middle Palaeolithic subsistence

Prior to OIS 3, one of the few dated faunal assemblages excavated comes from the Galeria Pesada, where Neanderthals or late *Homo heidelbergensis* consumed exclusively large game some 200,000 years ago (Marks et al 2002). Marks (2000) noted that Late Middle and Early Upper Palaeolithic sites are exceedingly rare in central Portugal and this suggests a very low population density. However, few palaeoenvironmental data exist for the latter part of Stage 3 and early Stage 2 making it difficult to know whether site density is due to geomorphic processes or reflects a human settlement pattern. Late Neanderthal subsistence in Portugal is poorly documented, mainly due to taphonomic, stratigraphic and dating problems. At the open-air site Foz do Enxarrique, large game dominates the faunal assemblage but the majority of the bones derive from non-cultural contexts stratigraphically below the arte-

Table 1 Select taxa reported from Late Middle and Upper Palaeolithic sites in central Portugal

| | Late Middle Palaeolithic | Gravettian | Solutrean | Magdalenian |
|-----------------------------------|--------------------------|------------|-----------|-------------|
| Large herbivores | | | | |
| <i>Cervus elaphus</i> | + | + | + | + |
| <i>Capreolus capreolus</i> | + | + | + | + |
| <i>Capra pyrenaica</i> | + | + | + | + |
| <i>Rupicapra rupicapra</i> | + | + | + | + |
| <i>Bos primigenius</i> | + | + | + | + |
| <i>Equus caballus</i> | + | + | + | + |
| <i>Sus scrofa</i> | + | + | + | + |
| <i>Dicerorhinus hemitoechus</i> | + | | | |
| <i>Stephanorhinus hemitoechus</i> | + | | | |
| <i>Elephas antiquus</i> | + | | | |
| Marine mammals | | | | |
| <i>Pusa hispida</i> | + | | | |
| <i>Delphinus delphis</i> | + | | | |
| Cetacea sp. | | + | | |
| Medium mammals | | | | |
| <i>Lepus europaeus</i> | + | + | | + |
| <i>Oryctolagus cuniculus</i> | + | + | + | + |
| <i>Castor fiber</i> | + | | | + |
| <i>Erinaceus europaeus</i> | + | | | + |
| Tortoises | | | | |
| <i>Testudo hermanni</i> | + | | | |
| <i>Emys orbicularis</i> | + | | | |
| <i>Mauremys leprosa</i> | + | | + | |
| Birds | | | | |
| <i>Gavia stellata</i> | + | | | |
| <i>Podiceps nigricollis</i> | + | | | |
| <i>Puffinus holeae</i> | + | | | |
| <i>Anas platyrhynchos</i> | + | | | + |
| <i>Melanitta nigra</i> | + | | | |
| <i>Melanitta fusca</i> | + | | | |
| <i>Clangula hyemalis</i> | + | | | |
| <i>Aquila chrysaetos</i> | + | | | |
| <i>Hieraaetus fasciatus</i> | + | | | |
| <i>Milvus migrans</i> | + | | | |
| <i>Falco cf. tinnunculus</i> | + | | | |
| <i>Alectoris rufa</i> | + | + | + | + |
| <i>Perdix perdix</i> | | + | | |
| <i>Grus primigenia</i> | + | | | |
| <i>Scolopax rusticola</i> | + | | | |
| <i>Numenius phaeopus</i> | + | | | |
| <i>Calidris canutus</i> | + | + | | |
| <i>Larus fuscus</i> | + | | | |
| <i>Pinguinus impennis</i> | + | | | |
| <i>Columba palumbus</i> | + | | | + |
| <i>Columba livia</i> | | + | | |
| <i>Bubo bubo</i> | + | + | | |
| <i>Athene noctua</i> | + | + | | + |
| <i>Asio flammeus</i> | | + | | |
| <i>Pyrhacorax pyrrhocorax</i> | + | + | + | + |
| <i>Pyrhacorax graculus</i> | | + | + | |
| <i>Corvus monedula</i> | + | + | | + |
| <i>Corvus corax</i> | | | + | |
| Corvidae | | + | + | + |
| <i>Pica pica</i> | | | | + |
| <i>Himantopus himantopus</i> | | | + | |
| <i>Gyps fulvus</i> | | | + | |
| <i>Aegyptius monachus</i> | + | + | + | |
| Passeriformes | + | | | |
| Fish | | | | |
| <i>Clupeia</i> sp. | | | | + |
| <i>Salmo</i> sp. | | + | | |
| Cyprinae | | | | + |
| <i>Sparus aurata</i> | | | | + |

Table 1 continued

| | Late Middle Palaeolithic | Gravettian | Solutrean | Magdalenian |
|----------------------------------|--------------------------|------------|-----------|-------------|
| Shellfish | | | | |
| Bivalvia | | | | |
| <i>Striarca lacteal</i> | + | | | |
| <i>Glycymeris glycymeris</i> | + | | | |
| <i>Cerastoderma edule</i> | | | | + |
| <i>Mytilus galloprovincialis</i> | + | | | |
| <i>Mytilus edulis</i> | | | | + |
| <i>Pecten maximus</i> | + | | | + |
| <i>Anomia ephippium</i> | + | | | |
| <i>Ostrea edulis</i> | + | | | |
| <i>Loripes lacteus</i> | + | | | |
| <i>Acanthocardia aculeate</i> | + | | | |
| <i>Parvicardium exiguum</i> | + | | | |
| <i>Laevicardium norvegicum</i> | + | | | |
| <i>Scrobicularia plana</i> | | | | + |
| <i>Lutraria lutraria</i> | + | | | |
| <i>Ervilia castanea</i> | + | | | |
| <i>Solen marginatus</i> | + | | | + |
| <i>Callista chione</i> | + | | | |
| <i>Tapes decussatus</i> | + | | | + |
| Gastropoda | | | | |
| <i>Patella vulgata</i> | + | | | + |
| <i>Patella ulyssiponensis</i> | + | | | |
| <i>Patella intermedia</i> | + | | | |
| <i>Patella rustica</i> | + | | | |
| <i>Gibbula cineraria</i> | + | | | |
| <i>Cerithium vulgatum</i> | | | | + |
| <i>Monodonta lineata</i> | + | | | + |
| <i>Monodonta colubrine</i> | + | | | |
| <i>Phasianella pullus</i> | + | | | |
| <i>Littorina saxatilis</i> | + | | | |
| <i>Littorina obtusata</i> | | | | + |
| <i>Charonia lampas lampas</i> | + | | | |
| <i>Trivia monacha</i> | | | | + |
| <i>Turritela</i> sp. | | | | + |
| <i>Semicassis undulata</i> | | | | + |
| <i>Thais haemastoma</i> | + | | | + |
| <i>Nassarius reticulatus</i> | + | | | + |
| Arthropoda | | | | |
| <i>Maja squinado</i> | + | | | |
| <i>Cancer pagurus</i> | + | | | |
| <i>Portumnus</i> sp. | + | | | |
| Echinodermata | | | | |
| <i>Paracentrotus lividus</i> | + | | | |

fact-bearing layer (Brugal & Raposo 1999). At Gruta Nova de Columbeira, large ungulates and carnivores dominate (Raposo & Cardoso 1998). Jiménez Fuentes et al (1998) reported a total of 338 tortoise remains, mostly of *Agrionemys* (= *Testudo*) *hermanni*. The assemblage from Gruta da Oliveira has been reported to have red deer, ibex, aurochs, rhino, horse, rabbit and tortoise (Angelucci & Zilhão 2009). At Figueira Brava, red deer, ibex and aurochs are the primary large mammals with fewer numbers of horse, rhino, elephant and wild boar. Only a few terrestrial carnivore bones were found including leopard, lynx, wild cat, wolf, fox and brown bear. Taphonomic analyses were not conducted and the 'rich' bone tool industry described by Antunes

(2000b) is suspect.

Regarding potential small animal hunting during the Middle Palaeolithic of Portugal, the European land tortoise (*Testudo hermanni*) and European pond turtle (*Emys orbicularis*) and Mediterranean pond turtle (*Mauremys leprosa*) are known from the Late Pleistocene in Portugal (table 1). *Testudo* is present in Figueira Brava, Columbeira, Gruta da Furninha and at the Middle Pleistocene site Mealhada. A cut-marked tortoise scapula from Gruta da Oliveira suggests humans brought them to the site (Zilhão 2001). *Mauremys* is present at Mealhada as well. *Emys* is present at Figueira Brava. Several tortoise shell fragments were also recovered in the Galeria Pesada.

Table 2 NISP values for select faunal categories from Late Middle and Upper Paleolithic sites in Portugal

| | Late Middle Palaeolithic | | | Gravettian | | | | Solutrean | | | | Magdalenian | | |
|------------------|--------------------------|------------|----------------|------------|------------------------|-------------|-----------|-----------|-----------|-------------|-----------|-------------|-------------|--------------|
| | Caldeirão | Columbeira | Figueira Brava | Caldeirão | Buraca Escura | Lagar Velho | Picareiro | Anecriçal | Caldeirão | Lagar Velho | Picareiro | Caldeirão | Picareiro | Lapa do Suão |
| Large herbivores | 99 | 220 | 358 | 95 | 971 (129) ² | 72 (255) | 31 | 1,601 | 221 | 134 (1,282) | + | 93 | 447 (1,319) | 52 (286) |
| leporids | 806 | - | >100 | 1,553 | 4 | 1,336 (76) | >3,000 | - | 9,406 | 7,211 | 96 | 7,408 | 12,905 | 5,152 |
| Birds | 9 | - | 47 | 10 | 1 | 46 | 220 | - | 36 | 66 (94) | 3 | 28 | + | 118 |
| tortoises | - | 338 | 6 | - | - | - | + | - | 1 | - | - | - | - | - |
| Amphibians | - | - | 8 ¹ | - | - | 14 | + | - | - | 124 | - | - | - | - |
| fish | - | - | - | - | - | 1 | 1 (+) | - | - | (47) | - | 1 | 252 (1) | + |
| shellfish | - | - | ~900 | - | - | - | - | - | - | - | - | - | + | + |

¹ Totals for all amphibians include toads, frogs and salamanders

² All values in parentheses reflect unidentified large mammal bone counts

None of the occurrences have been confirmed as human food remains except perhaps Oliveira. De Lapparent-de Broin and Antunes (2000) state that *T hermanni* prefers Mediterranean-type warm, dry summers while *Emys* is at least compatible with the cold-indicator fauna, auk (*Pinguinus impennis*) and ringed seal (*Pusa hispida*). The Figueira Brava tortoises provide apparently contradictory paleoclimate indications or perhaps represent non-analogue conditions.

Birds are generally not well-documented in Middle Palaeolithic sites in Portugal but Mourer-Chauviré and Antunes (2000) report 30 species from Figueira Brava (table 1). The five most common birds present are *Puffinus holeae*, *Alectoris rufa*, *Larus fuscus*, *Athene noctua* and *Pyrrhocorax pyrrhocorax*. Once again there is no mention of taphonomic indications of whether human or non-human predators deposited the bones in the cave. Birds were relatively common in the Galeria Pesada, but none can be securely identified as human food waste (Marks et al 2002).

Figueira Brava offers tantalising evidence for late Neanderthal use of a broad range of coastal resources (Antunes 2000a). The Neanderthal deposits contain 36 species of marine invertebrates of which Callapez (2000) suggests mussel, limpet, clam and crab were used as food (table 1). Ringed seal, dolphin, rabbit and several species of rodents and bats were also recovered from Figueira Brava (Antunes 2000a; Jeannot 2000; Mein & Antunes 2000).

Rabbit remains are ubiquitous in Middle Palaeolithic contexts in Portugal, but Neanderthals did not appear actively to pursue them. Rabbits are apparently abundant (>100) at Figueira Brava, and are mainly represented by juveniles which probably indicates a spring harvest (Mein & Antunes 2000) if they represent human food debris. Rabbits were very abundant at the Galeria Pesada, but once again there is no definitive evidence that they were deposited in the cave by humans (Hockett 2007). Zilhão (2001) reports that the Caldeirão rabbit bones are more numerous than tortoise remains, but he does not indicate whether or not they were brought to the site by humans.

Overall, then, current evidence suggests that Neanderthals in Portugal ate primarily large game animals; the consumption of tortoises, birds, rabbits and some coastal resources including shellfish and maybe marine mammals is more problematic. There is no definitive evidence for the Middle Palaeolithic consumption of fish.

5 Early Upper Palaeolithic subsistence in Portugal

The recent excavation of a few Early Upper Palaeolithic sites and taphonomic analyses of those faunal assemblages have led to a much-improved understanding of subsistence in southwest Iberia during this transition period. Currently there are no reliable Aurignacian sites with fauna identified in central Portugal. The sole candidate is the cave site Pego do Diabo, which has questionable stratigraphic integrity and a carnivore-derived faunal assemblage (Valente 2001; Zilhão 1997). The Aurignacian in Portugal is debatable and it is possible that the earliest modern foragers entered the region with Gravettian technology (Aubry et al 2003; Bicho 2005; Zilhão 2006). Only three Gravettian and Solutrean faunal assemblages have been published in detail, and we are currently documenting Early Upper Palaeolithic subsistence at Picareiro Cave. Nevertheless, available results from Lagar Velho and Buraca Escura, Anecrial and Caldeirão show that rabbit, horse, red deer, ibex and chamois are commonly associated with Gravettian, Terminal Gravettian and Proto-Solutrean occupations (Davis 2002; Almeida et al 2006) (table 2). Davis (2002) suggested that carnivores such as hyena and leopards brought the majority of red deer and horse remains during the Middle and Early Upper Palaeolithic at Caldeirão since most of the specimens are from juveniles. Ibex is dominant in places like Anecrial, Buraca Escura and possibly Picareiro, because these sites are located in higher elevations or on steep valley slopes (Aubry et al 2001). At Lagar Velho, red deer, wild boar, roe deer and aurochs are present in low frequencies (Moreno-Garcia 2002). For

the six components reported, rabbit makes up between 84.7% and 100% of the identified faunal remains. A small number of undetermined bird bones were also recovered. During the Terminal Gravettian, rabbit is abundant in lower and upper elevation sites, including Anecrial and Picareiro (Almeida et al 2006; see table 3 below). Birds, including red-legged partridge and pigeon, are abundant and found with abundant charcoal in the pre-LGM Layer T at Picareiro Cave (tables 4 and 5), as well as at Caldeirão. Tantalising evidence for Terminal Gravettian coastal resource use comes from Lagar Velho where a cetacean vertebra was found 20 km inland (Moreno-Garcia 2002). Fish bones from a salmonid and unidentified smaller taxon have been recovered from the pre-LGM layers of Picareiro. Ornaments made from *Littorina obtusata* shells from several Gravettian and Solutrean sites provide additional evidence for coastal visits and thus, marine foods (see also Bicho et al 2003 for Gravettian shellfish accumulation at Vale Boi in southern Portugal).

The current evidence for Early and Mid-Upper Palaeolithic diet indicates a broader range of animals, seen primarily in the definitive exploitation of rabbit and possibly birds, fish and other aquatic food items compared to Middle Palaeolithic diets. Anatomically modern humans appear with a subsistence strategy already focused on exploiting small animals and perhaps plants. It is also apparent that the number of sites and components increased during this period when compared with the Late Middle Palaeolithic.

Straus et al (2000) attributed further increases in the numbers of sites per millennium between the Gravettian and Solutrean to increased population

Table 3 Mammals from the Middle and Early Upper Palaeolithic layers recovered from Picareiro Cave through the 2008 field season

| | T | U | Z | BB | EE | FF | GG | HH |
|--|---|---|---|----|----|----|----|----|
| Mammals | | | | | | | | |
| <i>Cervus elaphus</i> | + | + | + | | | + | + | + |
| <i>Capreolus capreolus</i> | | + | | | | | | |
| <i>Capra ibex/pyrenaica</i> | + | + | | + | | | + | |
| <i>Rupicapra rupicapra</i> | | + | | | | | | |
| <i>Sus scrofa</i> | | | | | + | | | |
| <i>Equus caballus</i> | + | | | | | | | |
| <i>Lynx pardina</i> | + | + | | | | + | | |
| <i>Oryctolagus cuniculus</i> | + | + | + | + | + | + | + | + |
| <i>Arvicola terrestris</i> | + | + | | | | | | |
| <i>Microtus</i> sp. cf. <i>lusitanicus</i> | + | | | | | | | |
| Amphibians | | | | | | | | |
| <i>Bufo bufo</i> | + | + | | | | | | |
| <i>Pelobates cultripes</i> | + | + | | | | | | |
| (+)= presence | | | | | | | | |

Table 4 Birds from the Middle and Early Upper Palaeolithic layers recovered from Picareiro Cave through the 2008 field season

| | R | S | T | U | V | W | Z | AA | DD | HH | NISP |
|-------------------------------|---|---|---|---|---|---|---|----|----|----|------|
| <i>Alectoris rufa</i> | | + | + | | | | | | | | 10 |
| <i>Alectoris/Perdix</i> | + | | + | + | | | | | | | 22 |
| <i>Perdix perdix</i> | | | + | + | | | | | | | 5 |
| <i>Columba livia</i> | | | + | | | | | | | | 7 |
| <i>Pyrhacorax pyrrhacorax</i> | | | + | | | | | | | | 9 |
| <i>Pyrhacorax graculus</i> | | | + | | | | | | | | 2 |
| <i>Corvus corone</i> | | | + | | | | | | | | 1 |
| cf. <i>Corvus monedula</i> | | | + | | | | | | | | 1 |
| Corvidae | + | | + | | | | | | | | 8 |
| <i>Garrulus glandarius</i> | | | + | + | | | | | + | | 3 |
| <i>Sturnus vulgaris</i> | | | + | | | | | | | | 1 |
| Crow/Pigeon/Partridge-sized | + | | + | + | | + | + | | | + | 139 |
| <i>Pluvialis apricaria</i> | | | + | | | | | | | | 2 |
| <i>Calidris canutus</i> | | | + | | | | | | | | 2 |
| <i>Turdus cf. pilaris</i> | | | + | + | + | | | + | | | 5 |
| Turtidae | | | + | | | | | | | | 1 |
| <i>Asio flammeus</i> | | | + | | | | | | | | 1 |
| <i>Athene noctua</i> | | | + | | | | | | | | 1 |
| Total | | | | | | | | | | | 220 |

(+) = presence

Table 5 Radiocarbon dates extracted from charcoal samples from the lower levels at Lapa do Picareiro

| Level | Lab No. | Uncalibrated | IntCal04 | CalPal ^a | Fairbanks ^b |
|-------|-------------|-----------------|-----------|---------------------|------------------------|
| M | Wk-16417 | 16,389 ± 110 BP | 19,500 BP | 19,649 ± 248 | 19,503 ± 60 |
| O | Beta-247965 | 17,480 ± 100 BP | 20,500 BP | 20,910 ± 314 | 20,666 ± 141 |
| R | UGAMS-03415 | 19,100 ± 70 BP | 22,540 BP | 22,919 ± 291 | 22,681 ± 105 |
| S | Beta-234371 | 19,290 ± 80 BP | 22,660 BP | 23,053 ± 268 | 22,910 ± 135 |
| T4 | Beta-208221 | 20,240 ± 110 BP | 24,100 BP | 24,186 ± 290 | 24,148 ± 130 |
| U | Beta-234373 | 22,560 ± 110 BP | | 27,294 ± 390 | 27,108 ± 179 |
| U | Beta-234374 | 22,590 ± 110 BP | | 27,319 ± 387 | 27,142 ± 180 |
| U | Beta-208222 | 22,660 ± 240 BP | | 27,341 ± 443 | 27,221 ± 303 |
| FF | Beta-247964 | 28,610 ± 300 BP | | 33,065 ± 472 | 34,003 ± 344 |

density brought on by the climatic downturn and use of Iberia as a human refugium during the LGM. Zilhão and Almeida (2002) offered an alternative explanation for increased numbers of sites (and thus people) at this time. They point out that most of the known Late Gravettian, Terminal Gravettian and Lower Solutrean sites are known from open-air locales and a few caves whereas the Middle and Upper Solutrean are only found in caves or isolated finds. Increased runoff due to sparse vegetation may have erased much of the latter Solutrean record in open-air contexts. Conversely, they argue that cryoclastic sedimentation in caves increased allowing for the preservation of

thick Solutrean deposits as at Caldeirão.

Another alternative may be that people actually utilised the interior less frequently during cold events, and this may be particularly the case for the interior uplands (Haws 2003; Hockett & Haws 2002). In this scenario, the coast was the primary settlement area and when people moved into the interior they occupied primarily lowland caves and shelters for greater protection. During the warmer periods, open-air settlements in the interior and uplands may have been more comfortable and these environments more productive. Because little to nothing is known about Gravettian or Solutrean coastal settlement in central

Portugal, these alternatives remain to be tested (Bicho & Haws 2008).

Although distribution maps show an increase in sites during the Solutrean in Estremadura (central region of Portugal), they are primarily caves that were excavated decades ago and whose faunal assemblages suffer from many biases in collection and curation. Only Caldeirão and Picareiro have stratified Middle and Upper Solutrean faunal assemblages in Estremadura. At Picareiro Cave, however, the fauna is sparse and lithics are rare, suggesting less frequent visits to near-abandonment of this high elevation site at this time. Davis (2002) observed a dramatic decrease in carnivore input between the Mousterian and Solutrean at Caldeirão. This is likely due to local extinctions and more intensive human occupation of the cave during the Last Glacial Maximum. Also at Caldeirão, rabbits are particularly abundant during the Solutrean (Davis 2002; Hockett & Haws 2002), while red deer is the most represented ungulate followed by ibex, horse, and chamois. In addition, the degree of bone fragmentation and percentage of unidentifiable bones increases between the Early and Late Upper Palaeolithic, which may indicate more intensive carcass utilisation than before. It may also reflect greater amounts of time spent in the cave given the reduction in carnivore populations and increased need for shelter from worsening climatic conditions. The Middle Solutrean level in the 'Hanging Remnant' at Lagar Velho also contains a highly fragmentary assemblage of rabbit, red deer, roe deer, horse and wild boar (Moreno-Garcia 2002). Rabbit comprises 86% and 98% of the total from two excavated components. Birds include five identified species and three additional ones attributed to family groups. Fish is also present but not analysed and published.

During the Magdalenian, caves and rockshelters in the limestone massif were repeatedly used as short-term carcass butchery and processing sites (Haws 2006). Red deer and rabbit hunting characterise Magdalenian subsistence in general (eg, Bicho et al 2006). In addition, wild boar was often hunted and may have been preferentially transported from most faunal-bearing sites. The Magdalenian faunal-bearing sites Caldeirão, Lapa do Picareiro, Lapa do Suão and Lapa dos Coelhoos all have evidence for intensive large game carcass fragmentation indicative of marrow extraction and bone-grease processing. Rabbit hunting and processing has been dis-

cussed in detail elsewhere by Hockett and Bicho (2000) and Hockett and Haws (2002). Lapa do Suão documents the hunting of ducks and partridges (Haws & Valente 2006). Picareiro has evidence for small fish such as sardine or shad (Bicho et al 2000, 2006). Gilthead was identified at Suão (Haws & Valente 2006).

6 Hunting, climatic variability and subsistence decision-making in southwest Iberia

The archaeofaunal record has been used to test the hypotheses put forth by several researchers that resource intensification and dietary diversification occurred in central Portugal as part of a pan-Iberian Tardiglacial phenomenon (Aura et al 1998; Aura & Villaverde 1995; Morales et al 1998; Straus 1992, 1995, 1996). Ungulate and rabbit carcasses, however, appear to have been utilised with the same level of intensity throughout the Upper Palaeolithic in central Portugal (Haws 2003, 2006; Haws & Hockett 2006; Hockett 2006; Hockett & Haws 2002). This pattern matches that seen in the Algarve, southern Portugal (Manne et al 2006) and Spanish Mediterranean Region (Aura et al 2002; Martínez Valle 1995, 2001; Pérez Ripoll & Valle 2001; Stiner 2003; Villaverde & Valle 1995; Villaverde et al 1997). Despite the fact that marine resources were transported inland in greater frequency at the Pleistocene-Holocene transition, their presence in earlier contexts shows that coastal resource utilisation is not only a Tardiglacial phenomenon. Rabbit hunting was a primary activity throughout the Upper Palaeolithic, and it now appears that the hunting of birds has occurred in Estremadura since at least the Terminal Gravettian and possibly the Late Middle Palaeolithic.

Millennial- and even centennial-scale climatic variability has become a dominant theme in palaeoclimatic research on the Late Pleistocene. Statistical uncertainties in radiocarbon dating make it very difficult to correlate palaeoenvironmental changes with the archaeological record. In most cases, the data are too coarse-grained to make definitive correlations with specific warm and cold cycles. If we step back and look at Late Pleistocene climate and palaeoenvironments, it is clear that long-term survival in the face of extreme variability would have necessitated a high degree of flexibility in diet choice. By adopting a broad, generalised diet, Upper

Palaeolithic people could have mitigated the fluctuations and perturbations in resource availability that came with rapid climate changes. Populations focused on ungulate resources, so well documented for Neanderthals across the rest of Europe (see Hockett & Haws 2005 for a review of the zooarchaeological and isotopic evidence), may have experienced boom and bust cycles as those resources fluctuated. Localised extinction of human populations may have been frequent during the Late Pleistocene for foragers who chose that nutritional pathway (Trinkaus 1995).

As noted above, we have argued that dietary diversity may have been one of the driving forces behind population growth during the Upper Palaeolithic (Hockett & Haws 2003, 2005). In 2003, we suggested that '(p)ositive changes in Paleolithic demography may have been the result of foragers diversifying their diet at specific places during specific time periods' (p 213). We used this approach to argue that modern humans were able demographically to replace Neanderthal populations because of their greater overall health, reproductive success and lower infant mortality. We (Haws & Hockett 2004:180) also pointed out that:

energy maximizing may inhibit population growth. In fact, a highly carnivorous diet is energy inefficient compared to an omnivorous one due to energy loss at each trophic level. Energy loss also limits population size, thus explaining why the highest-level carnivores are also the rarest animals. Humans feeding as top carnivores adapted to large game hunting would not have been able to grow their populations.

Thus, most Neanderthal populations in Europe would not have had the same population growth capabilities as AMHS. In many circumstances, dietary diversification should be a cause of population growth, not a result (Hockett & Haws 2003).

7 Implications

Recent faunal, stable isotope and trace element analyses suggest that Neanderthals in central and western Europe focused their subsistence on large mammal exploitation, while modern humans utilised a broader range of smaller mammals, birds, fish, shellfish and plants (Richards et al 2000, 2001). By generalising, modern humans had greater access to biomass and essential nutrients that enabled them to have greater reproductive success and expanding populations at the expense of local Neanderthal populations (Hockett & Haws 2005). On the Iberian

Peninsula, Neanderthal populations south of the Ebro River survived for thousands of years longer than in most of Europe. The persistence of Neanderthal populations in southern Iberia may have been due to a more generalised diet which enabled them to maintain a level of reproductive fitness that precluded modern human populations from establishing a niche in the region (Hockett & Haws 2003).

If we consider the archaeological record of subsistence in southern Iberia, it is apparent that Early Upper Palaeolithic people intensively exploited both large and small game animals. Rabbit and ungulate carcass utilisation practices from the Gravettian onwards show the same degree of intensive nutrient extraction as in the Late Upper Palaeolithic. Dietary diversity is evident from the Late Middle Palaeolithic. An important but often neglected factor in discussions of Upper Palaeolithic diverse diets is the potential use of plants, which are quality sources of micronutrients. Evidence for plant use only rarely survives taphonomic destruction. Biogeochemical analyses and starch grain studies will hopefully provide further details in the future because micronutrients critical to human foetal development and growth, as well as body maintenance and healing, are typically more abundant and more easily obtained from plant resources compared with animal carcasses. It is probably safe to say that a deep understanding of why AMHS replaced Neanderthals in Iberia and elsewhere in Europe will not be obtained until we can accurately interpret the contribution of plant and animal resources to the respective diets of both groups of humans. But if small animal hunting is a good proxy for the collection and consumption of a diverse set of plants, then it is likely that anatomically modern humans of the Early Upper Palaeolithic in Portugal exploited a diversity of both plant and animal resources.

So why did modern humans adopt diverse diets and intensively extract nutrients from existing resources? Kuhn and Stiner (2006) recently suggested that this adaptation may be due to differences in gender-based labour roles between Neanderthals and moderns. The Upper Palaeolithic dietary pattern may have emerged in the eastern Mediterranean basin where several biogeographic zones converge. This diverse landscape created economic opportunities for women and children that may have fundamentally altered human socio-economic organisation. If true,

then the unintended consequences of this social fabric provided AMHS foragers with greater intake of essential nutrients that set the nutritional framework for a demographic advantage over Neanderthals through improving reproductive success and possibly extending life expectancy rates.

As sites such as the Galeria Pesada show, the mere fact that a diversity of potential resources exist in a region does not mean that human societies took advantage of them (Hockett 2007). The Galeria Pesada contains a wide variety of large and small mammals, birds, and reptiles, yet the archaic humans who occupied the site apparently ignored this diversity to focus on large game hunting. Modern humans make dietary decisions about what to eat and what to ignore for an extremely wide variety of social and ecological reasons. Climate change can alter the numbers, types, densities, and seasonal availability of

resources, but human societies ultimately must make the choice to exploit them. Only then can these populations consistently consume the diverse suite of essential nutrients that can directly lead to enhanced reproductive success.

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