

Eels, Beavers, and Horses: Human Niche Construction in the European Late Upper Palaeolithic

By ANTONY G. BROWN¹, LAURA S. BASELL² and REBECCA FARBSTEIN³

[ABS] *This paper examines interactions between co-occupants of riverine niches in north-west Europe during the Late Upper Palaeolithic using both ecological and archaeological data. It is argued that consideration of both the Lateglacial record and autecology of eel, beaver and horse supports a reinterpretation of some famous but enigmatic panels of Magdalenian mobiliary art as representations of eel fishing, along with horse and beaver exploitation in disturbed riverine habitats. It is further suggested that this constitutes a humanly co-constructed niche in ecological, nutritional and symbolic terms, which was also particularly advantageous for human well-being and social development in this time and place.*

Keywords: niche construction theory, Magdalenian, nutrition, mobiliary art, sedentism

Anatomically modern humans can be viewed as *both* occupants of a wide variety of Late Pleistocene ecological niches and also as modifiers of those niches (Laland & O'Brien 2010). This paper examines the interaction between Magdalenian (17,000–12,000 BP) co-occupants of the riverine niches in parts of north-west Europe using both ecological and archaeological data. We go beyond a passive interaction between Late Upper Palaeolithic hominins and ecology to consider the creation and recognition of active and reciprocal ecological modifications as an application of niche construction theory (NCT; Odling-Smee *et al.* 2013). The functional context for this analysis is human survival and health, but the implications are behavioural and even cognitive. In this paper we first present key aspects of the ecology (cf. autecology) of the key non-human species in this niche before relating them to human behaviour as reflected by mobiliary art.

A recent analysis of the distribution of Lower Palaeolithic super-sites in southern England and northern France by Brown *et al.* (2013) has highlighted the location-specific importance of fat and carbohydrate in balancing protein intake, and the importance of critical nutrients such as vitamins C, D, E, and folate. The typical location of super-sites in the most nutritionally diverse locations in the interglacial landscapes of this region (namely the lowest freshwater reaches on braided floodplains) strongly suggested that sources of fats, carbohydrate, and critical nutrients may have been utilised from sources other than, or in addition to, large herbivores. It was also noted that humans co-inhabited this niche with a distinctive combination of flora and fauna including aquatic plants, beaver, and eel, as well as other fish and waterfowl. This zone also attracted the herbivores that butchery evidence suggests were the main target prey, particularly horse and deer.

However, for the Lower Palaeolithic, apart from tool type, palaeoecological data, and site distribution – all of which can have multiple drivers – there is little or no other behavioural information and, as yet, limited isotopic data (Bocherens 2015). Data from analysis of dental calculus for microfossils (pollen, chemical compounds, starch, phytoliths, micro-charcoal, and diatoms) is generating a wealth of fascinating information (Salazar-García *et al.* 2013; Hardy & Buckley 2013; Buckley *et al.* 2014; Power *et al.* 2015; Hardy *et al.* 2015; 2016; Radini *et al.* [in press](#)). However, how such data, particularly phytoliths, relates to overall diet over the lifetime is still being established and is complicated by factors such as differential preservation (Hardy *et al.* 2015; Power *et al.* 2015), difficulties of identification related to mastication damage (Shillito 2011), and the fact that these environmental signatures can become incorporated through breathing, eating, oral hygiene activities, and raw material processing. The analysis of faecal biomarkers is an emergent field, but the results cannot be resolved to species level (Sistiaga *et al.* 2014). More behavioural data exist for the Late Upper Palaeolithic (Late Upper Palaeolithic (LUP), c. 15–10 ka BP) where additional data sources include portable and fixed art, a wider range of perishable artefacts, and human isotopic data as well as reduced confounding factors as a result of higher chronological resolution and less post-depositional disturbance.

Human settlement of north-west Europe in the LUP over the area covered by the Magdalenian culture ([Fig. 1](#)) must be seen in climatic context with high spatial as well as temporal variation, with biomes varying from tundra to cool temperate forest. After the Lateglacial maximum (LGM) this variation includes the rapid melting of permafrost which had covered all the non-glaciated parts of the British Isles, central and northern-central France, and the Low Countries as well as the northern part of the European Plain eastwards. This had melted by the Termination 1a c. 16.6 ka BP (end of the Heinrich 1 event meltwater pulse) which was marked by rapid warming with July temperatures rising 2–5°C into the Lateglacial Interstadial (Windermere or Bølling Interstadial, Lotter *et al.* 2012). July temperatures show a declining trend of c. 2°C during this interstadial with increasing instability (ie, cold oscillations) culminating in the Lateglacial Stadial (Younger Dryas) before the rapid warming at the beginning of the Holocene at 11.7 ka BP (Walker *et al.* 2009).

Recent work by the INTIMATE project utilising tephrochronology (Blockley *et al.* 2012) has allowed regional event stratigraphies to be identified which although broadly phase-locked to the Greenland NGRIP ice core record do show significant variations which were manifest by regional to local variations in vegetation cover (Walker *et al.* 2012). The lack of well-developed soils and high rates of climate change promoted moderate to high ecological disturbance

regimes with a high prevalence of, what we would recognise today as, early successional stages. For example open shrublands and light or scrubby woodland dominated by pioneers, ruderals, and light-demanding herbaceous species (Peyron *et al.* 2005). Many of these species, now found as Arctic or Alpine plants, are calcicoles suggesting soils were far less acidified than they became in the early Holocene (Rhind & Jones 2003). One of the best Lateglacial records for Central France, La Taphanel, shows rapid variations in major taxa such as pine, juniper, birch, grasses, mugworts (*Artemisia*), and other herbs (eg, Chenopodiaceae, *Helianthemum*) reflecting rapid climate change from just after the LGM, through the Older Dryas, the Allerød-Bølling, the Younger Dryas, and finally rapid warming into the Preboreal (Ponel *et al.* 1990). These biomes had high herbaceous productivity which attracted, and may have been partly maintained by large herbivores, small mammals, and birds but are without an analogy today (Gill *et al.* 2012). Fire may also have played an important role in maintaining moderate to high disturbance regimes (Thonicke *et al.* 2005) and variations in lithology, geomorphology, and geo-hydrological conditions created locally variable vegetation patterns as has been shown for the Netherlands (Hoek 1997). Of particular importance here is the probably persistence of more climatically temperate refugia, so called cryptic refugia (Birks & Willis 2008), in valley floors dominated by willows, birch, hornbeam, and alder (Ponel & Cooper 1990).

Although this paper concentrates on the Magdalenian, the broader focus is on the wider interpretation of Palaeolithic artefacts and the relationship between different ‘actors’ within an ecological niche rather than an exhaustive survey of Magdalenian art. It is also important to note that ecological conditions through abrupt environmental transitions (AETs) were similar in other interstadials in the MIS 3 such as IS 7–IS 5 (van Andel & Davies 2003; Davies *et al.* 2014). Two of the first migrants into this region during de-periglaciation were the European eel (*Anguilla anguilla*) from the west (Atlantic) and the European beaver (*Castor fiber*) from the east and south, with wild horse (*Equus*) probably surviving the LGM throughout most of central to northern continental Europe (Bignon *et al.* 2005). By the Magdalenian (c. 17–12 ka BP) these three species were common throughout north-west Europe and formed part of the ecosystems that Magdalenian people occupied and interacted with.

[H1]EEL, BEAVER, & HORSE ECOLOGY

There are aspects of the species specific ecology (autecology) of eels, beavers, and horses that are of particular archaeological significance. Eels are ecologically and evolutionarily unusual fish which humans have always struggled to understand – Aristotle, for example, suggested that they generated spontaneously from mud as he could find no larvae (Tskamoto & Kuroki 2014). Although there are some 800 species of eel alive today, only the European freshwater eel (*Anguilla Anguilla* L. 1758) is commonly found in north-west European freshwaters. *Anguilla anguilla* is the only catadromous fish common in Europe descending rivers to the Sargasso Sea to spawn (Schmidt 1922) with the pelagic eggs and then larvae taking 3 years to drift with the North Atlantic Current back to the European shelf where they metamorphose into ‘glass-eels’ and then into elvers (‘civelles’ in France) before migrating upstream (Wheeler 1969). After living in rivers and lakes for 8–18 years they migrate downstream to begin their 6000 km journey to the Sargasso Sea where they spawn and die. The triggers for their spawning-migration as silver eels are not fully understood but appear to be influenced by declining day length (photoperiod), high rainfall, and a complex effect of the lunar cycle (Brujns & Durif 2009).

This life-cycle means that eel re-occupation of the region after the LGM would have been directly linked to the re-establishment of the Gulf Stream as the Polar Front retreated from 35°N to above 55°N in under 1000 years. This re-occupation would have occurred during the Lateglacial from glacial refugia in Iberia and, using palaeoecological data, Kettle *et al.* (2008) show that eel was present in central France by 19,000 BP, although not into the British Isles until c. 11,000 BP (Table 1). Although some may die during their period in rivers and lakes, most will die in the Sargasso Sea, which makes their presence on LUP sites more likely to be due to human activity than natural processes. Eels can also spread rapidly from river to river and to lakes due to their semi-amphibian capabilities. As shown in this interglacial the European eel can occupy a wide range of habitats spanning the marine–freshwater ecotone and this ecological plasticity (Vøllestad 1992) produces large variations in their stable isotopes values (Harrod *et al.* 2005). This also reflects the eel’s generalist diet being both carnivorous and a scavenger, with the ability to detect blood through its keen sense of taste. One of its main prey is bloodworm, although it eats fish and larvae and, indeed, almost all aquatic fauna (Sinha & Jones 1975). The eel’s semi-amphibian abilities to cross land and come out of water also allows it to feed on earthworms (Deelder 1985) and may be due to an overwhelming urge to migrate (Tesch 2003).

There are two other aspects of eel ecology which are particularly relevant to humans. First, eel is of high nutritional value being high in both protein (66 g per 100 g) and fat (42 g per 100 g) with high levels of polyunsaturated fat (0.95 g per 100 g). It is also high in several essential minor nutrients including potassium, phosphorous, iron, zinc and sodium, taurine, and vitamins A, B6, and B12. Eels are also high in docosahexaenoic acid (DHA) which has recently been strongly linked to human brain development both directly and indirectly through mother’s milk (Xiang *et al.* 2000; Brenna & Carlson 2014). The high nutritional value of eel was utilised in the medieval and post-medieval period in Europe when it became a major food source promoted by the Church and, later, a major source of nutrition for urban settlements (Bunting & Little 2005). Eels were the fall-back food of settlers in North America who faced starvation in AD 1620 but traded for them with Native American peoples (Prosek 2011). Secondly it is the only common fish species in Europe that is ichthyohemotoxic; its blood is toxic to mammals, including humans. However the poison, which is a protein (Yoshida *et al.* 2008) that cramps muscles including the heart, is broken-down by any cooking, exposure to gastric juices, or naturally a few hours after the eel has died (Halstead 1988; Auerbach & Halstead

2007). Experiments in the 19th century showed that just a few drops of fresh eel blood could kill a medium-sized mammal such as a dog (Anon 1899; Sato 1917; Keffer & Welsh 1936). In the early 20th century Charles Robert Richet tried to use it as a vaccine but found that it caused anaphylaxis, and more recently it has been trialled in both traditional Chinese and northern English folk medicine (Amin *et al.* 2003; Hatfield 2004). Although it may be difficult to prove its use on points of spears for hunting game it is a possibility and warrants further investigation.

Beavers (*Castor fiber* L. 1758) migrated back into north-west Europe as part of the development of riverine woodlands and would have established themselves quickly in most river systems during this period (Table 1) from glacial refugia in Spain and south-east France (Liarsou 2014). The basic biology and major role of beavers in modifying riverine habitats is described by Coles (2006) who also reviews their post LGM history from at least 15.5 ka BP and recent redating of museum bones has confirmed that beaver survived through the Younger Dryas cold stage in south-west England (Marr 2016). Recent work on beavers has shown that they are driven to dam running water through audible cues and in the absence of high levels of predation would come to a self-limiting density related to the density and gradient of streams (Meentemeyer & Butler 1999; Westbrook *et al.* 2011). There are many ways in which beavers would have been of high value to hunter-gatherers from the high thermal value of their dense pelts, to their meat which is equivalent in energy to a roe deer (Coles 2006). As Coles discusses there are many ways in which beavers would have been of high value to hunter-gatherers from the high thermal value of their dense pelts to their meat, which is equivalent in energy to that of a roe deer (Coles 2006). There is also ethnographic evidence of their castor sacs being used as they contain a substance with similar medicinal properties to aspirin (Kitchener 2001). Other ethnographic examples exist of hunter-gatherers using their hafted teeth and mandible as tools (Osgood 1940). One of their most valuable features may have been their tails which store fat and can be as much as 60% fat by weight during the winter (Kitchener 2001).

The wild ‘caballine’ horses of Lateglacial Europe which belonged to the species *Equus caballus* showed regional morphological variations which suggest they survived the LGM in mainland Europe rather than migrating in from the south or east (Bignon *et al.* 2005). Horse remains are found at most bone-rich Magdalenian sites indicating they were one of, if not the, prime prey species for humans (Nitecki & Nitecki 1987). These small sized horses were common in a variety of open habitats and their dentition suggests they were adapted to grazing rather than browsing (Mihlbachler *et al.* 2011). The high land cover of sedges and graminoids would have promoted large herds (Bignon *et al.* 2005). The challenges presented by hunting free running herds are best addressed by ambush hunting, as demonstrated by ethnographic analogy (Stiner 2002). While the earliest evidence for ambush hunting at 1.8 million years ago remains a matter of debate (Bunn & Pickering 2010; Bunn & Gurtov 2014; Pante *et al.* 2012), skeletal adaptations are consistent with modern human’s ability to throw at high speed (Roach *et al.* 2013). Good evidence also exists that Lower Palaeolithic hominins hunted horses cooperatively (Stiner *et al.* 2009), as exemplified by the scapula of a horse punctured by a wooden spear found at Boxgrove GTP17 (Roberts & Parfitt 1999) and the horses found in association with the famous Schöningen spears (Conard *et al.* 2015). Floodplains were an easy place to kill horses while they were drinking. Horses are not habituated to swimming and try to avoid it; if forced to swim, they are at their most vulnerable. Although the palaeoecological contexts of the examples given above support a floodplain ambush hunting scenario as early as the 500 ka BP, recent research has demonstrated that Schöningen was not a mass kill site and instead represents several separate episodes of hunting and butchery (Urban & Bigga 2015; Balter 2014). Interestingly, new research on the site sediments has demonstrated that the spears and horse remains were not deposited on dry land, but in the lake under 1–2 m of water (Urban & Bigga 2015). After 250 ka BP it is more widely accepted that ambush hunting would have been possible (Stiner 2002) and, certainly by the Magdalenian, horse and reindeer were dominant components of the diet (Kuntz & Costamagno 2011) and seem to have been symbolically embedded in Magdalenian lifeways in a way that is not apparent for earlier periods (Langley 2013). An alternative to ambush hunting may be corralling and even proto-domestication has been discussed for the Solutrean and Magdalenian (Lewis 2009).

By the early Magdalenian beaver, eel, and horse were ubiquitous and probably numerous in central France and common throughout the area by the middle–late Magdalenian (Table 1). Beavers are highly adaptable and this makes them in effect pioneer species (Liarsou 2014) and one which was almost certainly hunted (Petillon 2008). Recent evidence from the Caune de l’Arago shows that, by the Lower Palaeolithic (MIS 13), in southern France beaver was being systematically exploited for its skin and meat (Lebreton *et al.* 2017). The attraction of horses to water and their vulnerability near it, and the effect of beavers on Lateglacial river systems, are just two of the ways these species interacted with each other and impacted the floodplain environment. Geomorphological research has shown that floodplains in this period were covered by secondary channels (Brown 1995; Pastre *et al.* 2003; Lespez *et al.* 2015) and beaver damming of these channels would have increased the year-round water availability – effectively creating many lakes or ponds (Coles 2006). This would have increased habitats available for fish (Häglund & Sjöberg 1999), waterfowl, and amphibians. The increase in fish and other aquatic species would have increased eels in particular and ponding would also have attracted grazing herbivores, especially in drought periods. Such beaver-modified ecosystems would have been particularly attractive for humans who, if present in low numbers, could be regarded as a part of this ecological association. It is argued here that humans introduced another interaction between the species co-occupying this ecosystem through sophisticated food procurement strategies which would have, in turn, altered competitive conditions for plant growth as part of the constructed niche evolution (Allaby *et al.* 2015).

[H1] JETHNOGRAPHIC EVIDENCE OF EEL FISHING AND ECOLOGICAL SYMBOLISM

There are two principal methods of fishing for eels, both of which require only very basic equipment. The first method uses a long pole, called in English a 'poke pole' (Fig. 2). Generally, the long pole is over 2 m long and is used to flush out eels from behind rocks and in aquatic vegetation. Once flushed-out they can be caught by hand, a practice known by Maori peoples as 'bobbing, feeling and striking' or by the use of a basket or eel spear. The pole can have a variety of ends, such as a hook or loop, or it can be a simple point. The other technique involves placing a severed horse head in shallow water to attract eels, which enter the cranial cavity through the orifices, attracted by the smell of rotting flesh. As reported in Smart (2003), the horse head is placed in water during the evening and eels are squeezed out the following morning (Fig. 3). A single horse head can be used repeatedly until there is little flesh left (*ibid.*, 152–3). There is also evidence of ancient eel fishing techniques from non-European societies, particularly among the Maori peoples in New Zealand. A Maori myth proposes that eels could be attracted out of the water by small game, as depicted in a painting of a giant eel being caught at Tangahoe Lake, New Zealand painted by T. W. Downes in 1918. Maori eel hunters used both their hands and multi-tanged eel spears (*matarau*) and killing batons (*patu tuna*; Fig. 4) to kill eels, and they also constructed eel-weirs which are structurally very similar to natural beaver dams (Fig. 4). Although it is beyond the scope of this paper, baskets and weaving would have been helpful in trapping and transporting eels, and there is evidence of rope/cord from Lascaux (Lerroy-Gourhan & Allain 1998) and from earlier Gravettian sites from Europe (Adovasio *et al.* 1996; Soffer *et al.* 2000a; 2000b). This ecological zone would be the most resource-rich for basketry as withies (willow saplings), tall grasses, and reeds (Hurcombe 2014) would have been readily available. There is archaeological support for ethnographic evidence of eel-catching with poles and killing batons. 'Batons' or *Bâton de commandement* commonly found at Magdalenian and Cresswellian sites north-west Europe would have been suited for killing fish, eel, and other small game, and harpoon-like antler projectile points might have been similarly useful as well as final Upper Palaeolithic 'Lyngby Axes' (Langley 2014).

Until recently many aspects of eel, beaver, and horse ecology proved mysterious and/or remarkable to diverse cultures. The discovery of eels on land, but not on nights with a full moon (Brujij & Durif 2009); the movement of adult eels and fry through river mouths on full moons; their green glow (biofluorescence; Baker 2013); and the relatively long-lasting post-mortem convulsions which are similar to those of snakes (caused by muscle contractions) all engendered stories and myths. Even today, the unusual long-distance life cycle of the European eel is not fully understood (Baker 1978; Pfeiler 1986). Similarly, beavers are mythically significant to many cultures, as it is the only medium-sized mammal to produce complex structures, fell trees, and be semi-aquatic. Similarly ethnographic evidence from North America reveals a complex relationship between humans and beavers encoded in myth and metaphor (Dods 2003).

The symbolic importance of horse during the LUP is evidenced by the fact that they are by far the most dominant artistic subject, especially in the Magdalenian (Rice & Paterson 1996). Aspects of their ecology would have been noticeable to prehistoric hunter-gatherers, including their tight social grouping and mutual grooming behaviour. During the Magdalenian there is evidence for the careful placement of horse teeth and bones in hearths within the caves of Labastide and Erberua, at the open site of Pincevent (Bahn and Vertut 1988; Lewis 2009) and the horse 'totem' cave at Ekain in the Basque Region (Leroi-Gourhan 1968). Associations between horse and eel persist today; in English the black line down the back of a horse is known as an 'eel stripe' (Stachurska 1999) possibly because it was a common belief until the late 19th century that a long black horse-hair thrown into running stream instantly became a live eel (Righton & Roberts 2014).

[H1] ARCHAEOLOGICAL EVIDENCE OF LATE UPPER PALAEOLITHIC EEL, BEAVER, & HORSE

Eel bones are relatively uncommon archaeological remains and otoliths, which offer the best information about age, have yet to be reported at Palaeolithic sites (Kettle *et al.* 2008, 1320). Even in later prehistoric and into historic contexts, eel remains are very rare finds. For instance, there is written evidence of eel exploitation during the medieval period but the relative lack of their bones in the archaeological record suggests that their recovery is poor (Kettle *et al.* 2008) and also that preserving (eg, smoking) and consumption softens bones so they are ingested or unlikely to be preserved. Indeed in several cultures, including Japanese, eel bones are themselves eaten as a delicacy. However, a few Magdalenian sites have yielded isolated eel remains. Trou du Frontal (Belgium) yielded two dentaries and a caudal vertebra (van Neer *et al.* 2007, 8), and an eel 'fishery' at Grotta della Serratura (Italy) suggested exploitation of immature yellow eel during the spring (Kettle *et al.* 2008).

Human exploitation of beavers is known from as early as the Lower Palaeolithic in Southern France (Lebreton *et al.* 2017) and beaver remains are evident throughout the Upper Palaeolithic in this region. In contrast, beaver remains are evident throughout the Upper Palaeolithic. The Aurignacian archaeozoological assemblage from Mladec Cave (Czech Republic) provides some of the earliest evidence of beaver exploitation (Svoboda 2001) along with bones from Kent's Cavern, UK (Campbell 1977; Currant & Jacobi 2011). The important ornamental assemblage from the Mladec cave also includes nine perforated beaver teeth, at least one of which was excavated less than a metre from the famous human skull (Schwartz & Tattersall 2006; Antl-Weiser 2006), suggesting symbolic interest in this species. Noteworthy LUP zooarchaeological assemblages from north-west Europe with significant quantities of beaver remains include the Magdalenian assemblage from Le Morin, France (Boudadi-Maligne *et al.* 2012), the Federmesser assemblage from Andernach, Germany (Stapert & Street 1997, 179–80), and Dog Hole cave at Cresswell (Campbell 1977) and King Arthur's Cave in the Wye Valley, UK (Currant & Jacobi 2011).

Horse bones are ubiquitous throughout Palaeolithic archaeological horizons and the species is commonly represented in art, from the Aurignacian through the Magdalenian (eg, Graziosi 1960; Simões de Abreu & Bednarik 2000; Pigaud 2002; Stevens *et al.* 2009). During the Lateglacial, horse would have made up a significant component of human diet (Bignon & Turner 2003; Turner 2006). Rice and Paterson (1996) calculated that 43.7% of Palaeolithic engravings are of horses. There is also evidence that the horses frequently portrayed in Magdalenian art were illustrative of real herds of animals (Hodgson 2003).

[H1]MOBILIARY ART

At least four sites yielded mobiliary art that may offer evidence of human engagement with the beaver-eel-horse ecosystem and exploitation of these species. The first is the Magdalenian type-site of Abri de la Madeleine rock-shelter in the Vézère Valley in the Dordogne, first excavated in 1863–4 by Edward Lartet and Henry Christy and later by Denis Peyrony (in 1926) and dating largely to the late Magdalenian (*c.* 12,640–13,440 BP: Boyle 1994; Gambier *et al.* 2000; Maier 2015). The Abbé Breuil interpreted one of the many zoomorphic engravings executed on a so-called ‘*bâton de commandement*’, as a human representation, a snake or an eel, and two horse heads (Fig. 5). Marshack later described the same group of engravings more generally as a ‘complex composition of “obscure significance”’ (Marshack 1972, 208), and there are some discrepancies between Marshack’s (1972) and Breuil’s transcriptions of the eyes on the anthropomorphic engraving. However, their transcriptions of the horse heads and snake- or eel-like animal are in accordance with one another. Other thematic elements on this engraving include a suggestion of water or a stream (which Marshack interpreted as vegetation), and a human figurine holding a long stick, spear, or pole.

We propose a revised interpretation of this depiction in which the snake-like animal may instead be interpreted as a European eel. This engraving includes a series of marks that seem to depict the confluent dorsal-anal and caudal fins (dorsal and ventral) near the tail end of an eel. Furthermore, the width to length ratio of the engraved animal is closer to that of an eel than to that of a grass-snake (*Natrix natrix*), which would be the most likely common snake to be associated with rivers and wetlands. However, we have a very incomplete record of snakes and other herpetofauna for the Lateglacial in this region and snakes, like most of the herpetofauna, are thermophiles, require a long enough period of summer warmth (over 16°C) in order to incubate eggs (Gleed-Owen 1999). Three true snakes (*Natrix natrix*, *N. maura*, and *Vipera latasteri*) are known from Magdalenian levels at Gorham’s cave in Gibraltar (Blain *et al.* 2013) and it is assumed that Iberia was the nearest refugium for these species during the LGM. There is also evidence of snakes at two Magdalenian sites in the Pyrenees. At Bois du Cantet Cave, in the Hautes Pyrénées *Natrix* sp., *Zamenis longissimus* (Aesculapian snake), and *Vipera aspis* (European adder) were recorded, and at Malarode Cave, Pyrénées-Atlantiques remains of *Natrix* sp. (Bailon 1991; Bailon pers. comm. 2016). It therefore has to remain an open question as to whether snakes were present in sites further north such as Abri de la Madeleine although it is likely by the end of the Magdalenian they would have migrated into this area, assuming they had not survived in a local refugia (Stewart pers. comm.).

Although there is little definitive detail on the stick held by the anthropomorphic figure, it could depict either a poke pole for eel fishing or a harpoon. The downward orientation of the stick is strongly reminiscent of the way the eel poke pole is held and used. Marshack (1972) refers to two branches or leaves on the lower end of the pole, but in his drawing they are on opposing sides of the pole and quite uniform and symmetrical, so they might represent prongs on an eel spear, killing baton, or harpoon. This alternative interpretation leads, in turn, to a revised narrative for the whole engraving; it may depict humans exploiting eels using both a tool similar to a poke pole and horses’ heads as an eel trap. This implies that the engraving may not be just a random assemblage of representational elements but, rather, an intentional narrative of activities that held both practical and symbolic importance to Magdalenian culture.

From the same site there is also a ‘fish carved on reindeer antler’ on display at the Musée de Saint-Germain-en-Laye, (see <http://donsmaps.com/laugeriebasse.html>). We argue here that it is possible that this is also a representation of an eel, for two reasons. First, although the artefact is incomplete, the length and shape of the carved fish is more typical of an eel than other freshwater fish (although it could be argued that this shape was mandated by the morphology of the antler). Even if the shape of the depicted species was dictated in part by the material support, the rib depicted at the top of the body is more reminiscent of the dorsal fin of an eel than a pike, which would be the most likely alternative fish species.

Another baton from La Madeleine, curated at the British Museum, preserves four schematic engravings previously interpreted as ‘fish’ (Sieveking 1987, 21, pls 28–9) alongside and, in one case superimposed on, an engraving of a horse. Several of these engravings are sufficiently abstract that they might be equally interpreted as schematic depictions of eels, and the hatched marks are particularly reminiscent of the scales and markings on eels. A similar ‘ladder’ motif found on another baton from La Madeleine (Sieveking 1987, 20–1, pls 26–7) was interpreted in the *Reliquiae Aquitanicae* (1875) as a schematised fish. However, the elongated shape of this motif and the suggestion of a dorsal fin again introduces the possibility that it represents an eel. The horse muzzle overlaps the eel/fish motif, spatially reinforcing the association between these two species; to modern viewers, the eel might appear to be moving into or out of the horse’s head, similar to its expected behaviour while being trapped in a horse-head. There are also bevelled spear points from La Madeleine along with several harpoons and leisters from the site attesting to the importance of fishing to the site’s occupants.

At Grotte de Montgaudier, Charante, central France, a reindeer antler *baton de commandement*, found in 1886, was incised with depictions of two eels (whose fins are discernable), two eels, a fish, and vegetation and/or water (Fig.

6). It was first described 1887 by Albert de Nadaillac who clearly recognised the eels and regarded the site as late Magdalenian. The engraved baton was accompanied by pieces of ivory decorated with engravings and a pierced bone which was decorated with a frieze of three horses as well as perforated reindeer antlers decorated with two heads of goats (Airvaux 2002). It is relevant here that this site is only just above river level with the lower areas liable to flooding today.

An engraved bone from El Pendo, north-west Spain depicts a 'horse and a serpent associated with a set of linear marks' (Marshack 1972, 211). Pozzi (2004) has noted that the representations on harpoons rarely represent terrestrial animals, so this example is unusual. By contrast the representation of fish on Magdalenian harpoons is frequent, although many are stylised and schematic (*ibid.*). Again the shape of the serpent is far more like an eel and it does not display the markings and forked tongue seen on representations that are almost definitely snakes such as the engraved bone from Grotte de Lorthet in the foothills of the Pyrenees (Breuil & Saint-Périer 1927; Marshack 1972, 223). The linear marks are curved and could represent water by analogue with depictions such as the line angles on the horse, bison and fish engraving on the eagle bone from La Vache (Ariège) as interpreted by Marshack (*ibid.*, 275).

An enigmatic representation from the Grotte du Mas d'Azil, Ariège, depicts a horse's head with a thin irregular line emanating from its mouth (Fig. 7). This has generally been interpreted as grass or some form of foliage (Tyldesley & Bahn 1983). Although possible, this seems rather prosaic and it is argued here that an equally plausible interpretation is that this also represents horse-head eel fishing. This is further supported by the presence of a possible 'spear-thrower' from the site with an unusual form (Garrod 1955). The spear-thrower, illustrated in Piette (1907 pl. li, no. 2), is 21 cm long and is thought to represent an eel with a small fish's tail against its head (Piette 1907; Garrod 1955). It is made on reindeer antler and its use as a spear-thrower is considered dubious by Garrod for a variety of reasons; however, the representation of the eel remains significant, even if the purpose of the artefact remains enigmatic. An alternative interpretation of the artefact might be that this is instead a fishing device of some unknown function. Two other artefacts from Mas d'Azil reinforce the possible significance of horse heads in the trapping and fishing of eels. A famous spear-thrower from the site depicts three horses heads in various stages of life and death (Mas D'Azil Website 2012). It has been interpreted as a young horse, an older horse, and a horse skull. The horse skull depiction is particularly relevant to this discussion. Another sculpture fragment from Grotto du Mas d'Azil has similarly been interpreted in the past as a horse head with the flesh removed. Overall, the graphic juxtaposition of images of life and death may be related to meaning associated with the use of the spear-thrower in killing horses, but it should be noted that the same life-death relationship is present in the use of a carcass to attract eels. An association between fish and horses and vegetation is also seen at Cueva los Casares where there are also images of possible anthropomorphic mustelids, such as otters, but which could also be reinterpreted as beavers (Fig. 8, see below for further discussion of beaver/otter representation).

A strong association between fish and fertility is suggested at Bruniquel, Tarn-et-Garonne (Sieveking 1987), where a broken baton, which was carved to the shape of a phallus, was decorated with fish and 'angles probably representing water' (Marshack 1972, 330). A broken engraved bone from the same site is interpreted as a depiction of fish on one side and uncertain images, fish tails, or trees on the other. An alternative interpretation is that these are fish or eel heads and the uncertain images are eel spears, similar to those used by Maori, or a fish-catcher (*ibid.*, 200).

Several other sites have depictions that might be related. A rib bone from La Vache, in the French Pyrenees, was engraved with a horse head, which Marshack (1972, 225) interpreted as a stallion, followed by a mare; the two figures are separated by a symbolic branch. However, Marshack does not discuss the curved line emanating from the stallion's mouth which might be a schematic interpretation of an eel. Mobiliary art from other sites associates horses or horse's heads with rivers and fish. For instance, an engraving on stone from Trois Frères (Ariège) features a small horse's head engraved over a fish (Marshack 1972, 244). Similarly, an engraving on a baton from Abri Mège, Teyjat, depicts a horse and deer head surrounded by three serpentine shapes (*ibid.*, 260). At least one of the shapes has a pectoral fin while another has a clear lateral-line, suggesting that they are probably depictions of eels rather than snakes. At Grotte de Raymond, Chancelade (Dordogne), a stone baton was engraved with a horse's head, fish, harpoon, and a possible bud or flower (Breuil 1937; Marshack 1972; Tyldesley & Bahn 1983).

While evidence for the use of beaver pelts exists from at least the Middle Palaeolithic (Fiore *et al.* 2004), there are only a few possible depictions of beavers in Magdalenian art. One of them comes from Abri de la Madeleine regarded by the Musée Les-Eyzies-de-Tayac as an anthropomorph entitled 'The sorcerer of La Madeleine' (Fig. 9). The other is a very well known engraved image of two women-otter figures from the Middle Magdalenian levels at Isturitz (on display at the Musée Nationale de Préhistoire Les Eyzies de Tayac; Isturitz Websites). Both images have traditionally been regarded as human-otters and, in the La Madeleine case, an otter-like human/shamanistic being (Cooper 2001). However, this figure (Fig. 9) appears to have a wide/fat tail and the other has a similar body shape and either no tail or possibly a fat tail rendered as feet. In these regards, both images are more likely to be beavers than otters, in which case a symbolic link is suggested between the human form (and/or human behaviour) and beavers. The presence of beaver in the region during the Magdalenian is not in doubt (see Table 1), however, there is only one find of fossil otter (*Lutra lutra*) from the Lateglacial in France and that comes from the Alps (Chaix & Olive 1984) although finds are known from Germany and Poland (Knul pers. comm.). Although it might be argued that otter would likely be under-represented in caves and not being a human food resource (like most carnivores) there is no fossil data at present to question the view of Sommer and Beneck (2004) that the European population of otter was restricted to a single glacial refuge and did not expand westwards into France until the Holocene. Other purported otter representations might

be similarly reconsidered as beavers. For instance, an engraving from Laugerie Basse, Dordogne, repeatedly interpreted as an otter, is located adjacent to one fish engraving and overlapping another (MacCurdy 1924, 37; Guthrie 2006, 224). Like the other enigmatic zoomorphs discussed above, the purported ‘otter’ is easily re-interpretable as a beaver.

[H1] NICHE CONSTRUCTION THEORY & LATEGLACIAL HUMAN-ENVIRONMENT INTERACTIONS

Niche construction theory (NCT) provides a potentially valuable framework for analysing the bi-directional interactions of humans with environments in the past which explicitly considers human behaviour, abiotic factors, and ecological feedbacks within an evolutionary context (Smith 2007; Lewontin 2000; Odling-Smee *et al.* 2013; Allaby *et al.* 2015). Niche construction refers to the ‘modification of both biotic and abiotic components in environments via trophic interactions and the informed (i.e., based on genetic or acquired information) physical work of organisms’ (Odling-Smee *et al.* 2013, 5). Of importance here is that this includes both actions by humans and also by other biotic components of the ecosystem. It is evolutionary in that it can increase carrying capacities, facilitate co-operative behaviour, and lead to ecological inheritance which can include acquired social learning. This includes an element of *selective pressure* provided by a diet that would enhance brain development in infants and facilitate cognition, rapid learning, and visual acuity (Cheetham *et al.* 2006; Agostini 2008). NCT goes beyond the extended phenotype approach (*sensu* Dawkins 1982) in considering such behaviour as more than adaptations, including by-products such as artefacts that include signs, signals, or new behaviours which may or may not be ‘profitable’ (Madden *et al.* 2012). In both evolutionary and archaeological terms NCT is important because it can; (a) influence the strength and selection acting on all participants (Odling-Smee *et al.* 2003), (b) increase the abundance of individuals by increasing fecundity and/or extending longevity, and (c) encompass ecological spill-overs which are modifications to other species niches creating multiple co-evolutionary events. NCT also implicitly recognises ecological change through the occurrence of new assemblages creating potentially novel trophic interactions as must have been common under the rapidly changing climates and biogeographical biotic distributions during periods of rapid climate change such as the Late Upper Palaeolithic (Dawson *et al.* 2011; Birks & Birks 2008). Thus particular associations brought into being by climatic change can interact to produce locationally-specific nutritional advantages for human populations, in this case along river-corridors. Of particular significance for this paper is the commonly cited example in the NCT literature of the beaver’s dam which alters the environment of many populations and even the abiotic environment (Naiman *et al.* 1988; Odling-Smee *et al.* 2003). We can also differentiate niche construction (as with the beaver dams), opportunistic niche recognition via inherited environmental knowledge and niche maintenance through repeated use involving social memory.

[H1] INTERACTION, NICHE CONSTRUCTION, & DISCUSSION

The re-interpretation of some panels of mobiliary art as possible depictions of interactions between eels (and in some cases fish), horses, and in a few cases beavers highlights the interactions between these species and Magdalenian hunter-gatherer-fishers. The similarity between fish or eel killing batons, bâton de commandement and bâton perforé should be explored more although they have been interpreted in a bewildering number of ways (Bahn & Vertut 1988). It is also during the Magdalenian that harpoon technology becomes widespread (Julian 1982). It is not clear what the prey species were, but a link with fishing is most commonly made (Julien 1982; 1995; Román and Villaverde 2012) although this is difficult to prove due to the lack of detailed studies of ichthyofauna.

In the riverine environments of mainland north-west Europe along with the niche constructing activities of beavers we can add the involvement of Magdalenian peoples through butchery by rivers (attracting eels), and the hunting/trapping of eels and beavers (Fig. 10). This niche co-constructed by humans and beavers would have produced ecological spill-over effects of increases in waterfowl and fleshy tubers such as reed-maces (*Typha* sp.). In this context it is interesting to note that the highest proportion of all birds represented in art are water-birds such as swans, geese, ducks, and heron (Bahn & Vertut 1988). This niche can also be seen in relation to evolving views on Magdalenian diet and nutrition as counterbalancing potentially excess protein in the Magdalenian diet (Speth 1991). Whilst the Magdalenian in north-west Europe has commonly been viewed as the ‘reindeer-horse hunters’ with regional variations (Ávarez-Fernández 2011) this is biased by the data which are largely artefacts, animal bones, and a limited amount of isotopic data. Recent studies using different datasets such as dental calculus have argued for a much broader dietary base including significant plant consumption including underground storage organs (Power *et al.* 2015). This study also recovered a sponge spicule from dental calculus suggesting some plant or animal input from a freshwater habitat.

This can be seen as part of the co-evolution of plant-human relationships (Allaby *et al.* 2015) and which we argue here includes co-constructed riverine niches. These niches would also have been relatively stable in the face of climatic instability during this period (Bignon *et al.* 2005) and may have provided an expanded season of both protein and carbohydrate/fat. Any linkage between the exploitation of individual resources inevitably raises the question of seasonality. It has been argued that, in the Magdalenian in France, reindeer was hunted in the autumn/winter and horse in the spring/summer (Fontana 2000). There is direct evidence of reindeer hunting in autumn from Verberie in northern France (Enloe 2006). If so, a link between the exploitation of horse and eel would suggest a spring to summer window, however, both eel and beaver are potentially available year-round. Beavers do not hibernate but store enough wood underwater to last the winter, which they can access even if the pond or river is frozen over and snow cover has made terrestrial plants inaccessible. Ethnographic records from North America indicate that beaver tail fat provided an important late winter fat component for human diet (Coles 2006). Winter availability also applies to several plant

resources such as the rhizomes of reed-maces and the leaves of plants such as watercress (*Rorippa nasturtium aquaticum*) which are high in valuable nutrients, particularly vitamin C. Although it is difficult to be precise about the targeted species, the noted rise of harpoons as an artefact type during this period reinforces the centrality of riverine environments (Julien 1982; 1995; Román & Villaverde 2012). This accords well with Boyle's (2010) argument in favour of true specialisation during the Magdalenian and Solutrean, and it is possible to see how this adaptation could fit into arguments regarding the expansion of the Magdalenian to north-west Europe (Miller 2012).

It is proposed here these relationships, between eel, beaver, horse, and Magdalenian peoples constitute a humanly-constructed niche in both ecological and symbolic terms, which was also advantageous for human well-being and social development in at least two ways. First it allows year-round occupation which has reproductive, social, and cultural consequences (Shennan 2001; Zubrow 2010). Secondly the diet, and in particular the high consumption of eels, eggs, and fish would be unusually high in long-chain polyunsaturated acids (LCPs, including omega-3 and omega-6) and docosahexaenoic acid (DHA). These nutrients are all known to promote eye and brain development in babies and social learning (Xiang *et al.* 2000; Brenna & Carlson 2014; Birch *et al.* 2007; Kuratko *et al.* 2013). In terms of culture and to paraphrase Lévi-Strauss (1964), food and cooking is a language – and an essential part of group identity and culture. Both the sedentism and the nutritional advantages are part of the ecological feedbacks and selective pressure within an evolutionary context that underlie niche construction theory (Smith 2007; Lewontin 2000; Odling-Smee *et al.* 2013; Allaby *et al.* 2015) and simultaneously can be seen as part of the way human agency was created and transformed through inhabitation of complex material conditions (Barrett 2001). We suggest here that the representation of the affluence and development of such a society is embodied in the symbolism of the artistic representations discussed here.

[H1]CONCLUSIONS

It is argued here from a combination of ecology, palaeoecological evidence, and the reinterpretation of several pieces of mobiliary art that Magdalenian hunter-gatherers had honed the skill set and technologies necessary to undertake eel-fishing using poke poles, nets, or baskets, and horse heads used as traps. These innovations which are part of the 'broad spectrum evolution' could have arisen when eels were attracted to horse butchery sites in shallow channels and on river banks, and the roots of these practices might extend even earlier in the Palaeolithic. This can also be seen as part of a larger socio-ecological interaction between humans and beavers, with horses and eels (as beaver dams are ready-made eel traps and ideal for horse-head eels traps) which, we argue, formed part of a particularly valuable and probably symbolically loaded humanly constructed niche. The similarity between hedge-type fish traps now known to date from at least the early Mesolithic in north-west Europe (Zvelebil 2008; Smart 2003; Zhilin 2014) suggests this niche construction could have been an integral part of associative innovation which extended north during the Magdalenian. Both the act of depicting eels, horses, and beavers as elements on mobiliary art at sites with other elements of ritual significance, and the biology of these three animals (which have engendered myths until the present day), suggests that they were part of an animistic association which represented important elements of the Magdalenian peoples' view of both themselves and other occupants of this ecological niche. This also implies that key panels of Magdalenian mobiliary art could be seen as representing ecological assemblages and a constructed niche rather than isolated biological, resource, or symbolic elements. Seen as such, this is part of the deeper time-depth of co-evolutionary process with selective pressure that led eventually to domestication of key species such as the horse (Allaby *et al.* 2015). This behaviour is also part of an evolving socio-ecological cognition that some have argued forms part of modern human behaviour.

However, the existence of this ecological association earlier in the Pleistocene, but relative lack of artistic representation, cautions against such an interpretation. Indeed, whilst the primary focus for this paper has been on the Magdalenian, there is intriguing evidence that the association of hominins in this particular niche may have much deeper roots. For example, the site of Cueva Millán dating to 37,600 BP yielded six species of fish including trout (*Salmo trutta fario*, N=198), Iberian nase (*Chondrostoma toxostoma*, N = 52), and eel (*Anguilla anguilla*, N = 29) in association with human activity (Izquierdo 1992; Boyle 2010). Even older is the remarkable 2012 discovery of the Eemian site of Waziers, France (minimum U/Th age of 103±3.5/–3.4 ka, Hérissou *et al.* 2015) where wood shows clear marks of beaver activity and a cut mark on one of the beaver bones (*Castor fiber*) (Hérissou pers. comm. 2015). Although analysis is still underway, a range of other interglacial fauna were also present including horse, roe and red deer (Hérissou pers. comm. 2015). Whilst we can never put ourselves in the place of these Palaeolithic peoples and the use of ethnographic analogy such as Maori or even historical eel fishing should be used with care (Lane 2014), a holistic approach to understanding their artefactual remains and landscapes surely places some constraints on the plethora of possibilities and can only improve our interpretations of artefactual evidence. Re-interpreting some key Palaeolithic art objects also highlights the importance of studying Palaeolithic art in its broader ecological and archaeological context, rather than continuing to focus on the iconographic features and interpret them in isolation.

[9P]Acknowledgments: Thanks to John Stewart, Chris Glead-Owen, Mark Roberts, Kathryn Boyle, William Davies, John Stewart, Monika Knul, Mike Lobb, Kevin Walsh, Mark Gardiner, Finbar McCormick, Extra Zubrow, and Des Tatana Kahotea for helpful discussions on this topic which improved the paper. Thanks also to Don Hitchcock for assistance with photographic materials.

[H1]BIBLIOGRAPHY

[BIBL]Aaris-Sorensen, K. 2009. Fossils and strata, diversity and dynamics of the mammalian fauna in Denmark throughout the last glacial interglacial cycle 115–0 BP. *Fossils and Strata* 57, 1–59

- Adavasio, J.M., Soffer, O. & Klima, B., 1996. Upper Palaeolithic fibre technology: interlaced woven finds from Pavlov I, Czech Republic, c. 26,000 years ago. *Antiquity* 70, 526–34
- Agostoni, C. 2008. Role of long-chain polyunsaturated fatty acids in the first year of life. *Journal of Pediatric Gastroenterology & Nutrition* 47 Suppl. 2, S41–4
- Airvaux, J. 2002. *L'art préhistorique du Poitou-Charentes*. Paris: Editions La Maison des Roches
- Allaby, R. G., Kistler, L., Gutaker, R.M., Ware, R., Kitchen, J. L., Smith, O. & Clarke, A.C. 2015. Archaeogenomic insights into the adaptation of plants to the human environment: pushing plant–hominin co-evolution back to the Pliocene. *Journal of Human Evolution* 79, 150–7
- Amnin, C., Yingfu, M., Yuan, G. & Zhemin, G. 2003. *Encyclopedic Reference of Traditional Chinese Medicine*. Heidelberg: Springer
- Andel, T.H. van & Davies W.D. (eds). 2003. *Neanderthals and Modern Humans in the European Landscape of the Last Glaciation – Archaeological Results of the Stage 3 Project*. Cambridge: McDonald Institute for Archaeological Research
- Anon, 1899. Poison in the blood of the eel. *New York Times* 9 April 1899.
- Antl-Weiser, W. 2006. Szombathy's excavations in the Mladec cave and the first presentations of the results. In M. Teschler-Nicola (ed.), *Early Modern Humans at the Moravian Gate: Mladec Caves and their Remains*, 1–16. Vienna/New York: Springer.
- Auerbach, P.S. & Halstead, B.W. 2007. Hazardous aquatic life. In P.S. Auerbach & E. C. Geehr (eds), *Management of Wilderness and Environmental Emergencies*, 933–1028. St louis: C.V. Mosby (2 edn)
- Ávarez-Fernández, E. 2011. Humans and marine resources interactions reappraised: archaeofauna remains during the Late Pleistocene and Holocene in Cantabrian Spain. *Journal of Anthropological Archaeology* 30, 327–43
- Bahn, P. & Vertut, J. 1988. *Images of the Ice Age*. New York: Windward
- Bailon, S. 1991. *Amphibiens et Reptiles du Pliocène et du Quaternaire de France et d'Espagne: mise en place et évolution des faunes*. Unpublished M.S. thesis, Université Paris 7
- Baker, M. 2013. First fluorescent protein identified in a vertebrate. *Scientific American*
<https://www.scientificamerican.com/article/first-fluorescent-protein-identified-in-a-vertebrate-animal/>
- Baker, R. R. 1978. *The Evolutionary Ecology of Animal Migration*. New York: Homes and Meier
- Balter, M. 2014. The killing ground. *Science Magazine* 344, 1080–3
- Barrett, J. 2001. Agency, the duality of structure, and the problem of the archaeological record. In I. Hodder (ed.), *Archaeological Theory Today*, 141–64. Cambridge: Cambridge University Press
- Barton, N., Roberts, A.J. & Roe, D.A. 1991. *The Lateglacial in North-west Europe: Human Adaptation and Environmental Change at the End of the Pleistocene*. York: Council for British Archaeology Research Report 77
- Bignon, O. & Turner, E. 2003. *Horse Hunting and the Utilization of Horse Carcasses during the Magdalenian in Europe*. Oxford: British Archaeological Report S65
- Bignon, O., Baylac, M., Vigne, J-D. & Eisenmann, V. 2005. Geometric morphometrics and the population diversity of Lateglacial horses in Western Europe (*Equus caballus acerelini*): phylogeographic and anthropological implications. *Journal of Archaeological Science* 32, 375–91
- Birch, E.E., Garfield, S., Castaneda, Y., Hughbanks-Wheaton, D., Uauy, R. & Hoffman, D. 2007. Visual acuity and cognitive outcomes at 4 years of age in a double-blind, randomized trial of long-chain polyunsaturated fatty acid-supplemented infant formula. *Early Human Development* 83, 279–284
- Birks H.J.B. & Birks H.H. 2008. Biological responses to rapid climate change at the Younger Dryas–Holocene transition – succession, diversity, turnover, and rates of change. *Holocene* 18, 19–30
- Birks, H.J.B. & Willis, K. 2008. Alpines, trees, and refugia in Europe. *Plant Ecology and Diversity* 1, 147–60
- Blain, H-A, Gleed-Owen, C., Carrión, J. S., Jennings, R., Finlayson, G. & Giles-Pacheco, F. 2013. Climatic conditions for the last Neanderthals: Herpetofaunal record of Gorham's Cave, Gibraltar. *Journal of Human Evolution* 64, 289–99
- Blockley, S., Bourne, A., Brauer, A., Davies, S.M., Hardiman, M., Harding, P.R., Lane, C.S., MacLeod, A., Matthews, I.P., Pyne-O'Donnell, S.D.F., Rasmussen, S.O., Wulf, S. & Zanchetta, G. 2012. Tephrochronology and the extended intimate (integration of ice-core, marine and terrestrial records) event stratigraphy 8–128 ka b2k. *Quaternary Science Reviews* 106, 88–100
- Bocherens, H. 2015 Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. *Quaternary Science Reviews* 117, 42–71
- Bocquet, A. 1969. L'Isère préhistorique et protohistorique. *Gallia Préhistoire* 12(1), 121–400
- Boudadi-Maligne, M., Mallye, J.-B., Langlais, M. & Barshay-Szmidt, C. 2012. Magdalenian dog remains from Le Morin rock-shelter (Gironde, France). Socio-economic implications of a zootechnical innovation. *Paleo* 23, 39–54
- Boyle, K.V. 1994. La Madeleine (Tursac, Dordogne). Une étude paléoeconomique du Paléolithique supérieur. *Paleo* 6, 55–77
- Boyle, K.V. 2010. From laugerie basse to jolivet: The organization of final Magdalenian settlement in the Vézère valley. *World Archaeology* 27, 477–91
- Bozinski, G. 1979. Stratigraphie du Paléolithique supérieur récent et du Paléolithique final dans le bassin de Neuwied (vallée du Rhon moyen RFA). In de Sonnerilles-Brodes, D. (ed.), *Le Fins des Temps Glaciaires en Europe*, 193–201. Paris: Colloques Internationaux du CNRS 271
- Bosninski, G. 1983. Die Jägerische geschichte dew Rheinlandes – einsichen und lucken. *Jahrbuch des Romisch-Germanischen Zentralmuseums Mainz* 30, 81–112
- Brenna, J.T. & Carlson, S.E. 2014. Docosahexaenoic acid and human brain development: Evidence that a dietary supply is needed for optimum development. *Journal of Human Evolution* 77, 99–106
- Breuil, H. 1937. *Les Subdivisions du Paléolithique Supérieur et leur Signification* (2 edn)
- Breuil, H. & Saint-Périer, R. 1927. *Les poisons et les reptiles dans l'art quaternaire*. Archives de l'Institut de Paléontologie Humaine. Paris: Institut de Paléontologie Humaine Mémoire 2
- Brochier, J.E. & Livaxhe, M. 1978. Le niveau C de l'abri n°1 de Chinchon à Saumane de Vaucluse: analyse des correspondances et ses conséquences quant à l'origine des complexes du Le niveau C de l'abri n°1 de Chinchon à Saumane de Vaucluse. *Géologie Méditerranéenne* 4, 359–69
- Brown, A.G. 1995. Lateglacial–Holocene sedimentation in lowland temperate environments: floodplain metamorphosis and multiple channel systems. *Palaeoclimate Research/ Paläoklimaforschung* 14, 1–15

- Brown, A.G., Basell, L.S., Robinson, S. & Burge, G.C. 2013. Site distribution at the edge of the Palaeolithic world: A nutritional niche approach. *PLoS ONE* 8(12), e81476, 1–14
- Brujls, M.C.M. & Durif, C.M.E. 2009. Silver eel migration and behaviour. In Van den Thillart, G., Dufour, S. & Rankin, J.C. (eds), *Spawning Migration of the European Eel*, 65–95. Amsterdam: Springer
- Buckley, S., Usa, D., Jakob, T., Radini, A. & Hardy, K. 2014. Dental calculus reveals unique insights into food items, cooking and plant processing in prehistoric central Sudan. *PLoS ONE* 9(7), e100808.
- Bunn, H.T. & Pickering, T.R. 2010. Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running-hunting and passive scavenging by early Pleistocene hominins. *Quaternary Research* 74, 395–404
- Bunn, H.T. & Gurtov, A.N. 2014. Prey mortality profiles indicate that Early Pleistocene Homo at Olduvai was an ambush predator. *Quaternary International* 322–3, 44–53
- Bunting, S.W. & Little, D. C. 2005. The emergence of urban aquaculture in Europe. In B. Costa-Pierce, A. Desbonnet, P. Edwards & D. Baker (eds), *Urban Aquaculture*, 119–37. Wallingford: CAB International
- Burkitt, M.C. 1921. *Prehistory: A study of early cultures in Europe and the Mediterranean Basin*. Cambridge: Cambridge University Press
- Campbell, J. B. 1977. *The Upper Palaeolithic in Britain: A study of man and nature in the Late Ice Age*. Oxford: Clarendon
- Chaix, L. & Olive, C. 1984. Étude de la faune de l'Épipaléolithique à la Tène. *Bulletin de la Société Préhistorique Française*, 81, 337–341.
- Cheatham, C.L., Colombo, J. & Carlson, S.E. 2006. n-3 Fatty acids and cognitive and visual acuity development: methodologic and conceptual considerations 1'2'3'4. *Am J Clin Nutr* 83 no. 6, S1458–1466S.
- Clark, J.G.D. 1936. *The Mesolithic Settlement of Northern Europe*. Cambridge University Press, Cambridge.
- Coles B. 2006. *Beavers in Britain's Past*. Oxford: Oxbow Books.
- Conard, N.J., Jordi Serangeli, J., Böhner, U., Starkovich, B.M., Miller, C.E., Urban, B. & Van Kolfschoten, T. 2015. Excavations at Schöningen and paradigm shifts in human evolution. *Journal of Human Evolution* 89, 1–17
- Cooper, M. 2001. *Exploring the Ice Age*. London: Atheneum
- Cordy, J.-M. 1991. Palaeoecology of the lateglacial and early postglacial of Belgium and neighbouring area. In Barton *et al.* (eds) 1991, 40–7
- Couloonges, L. 1963. Magdalénien et périgordien post-glaciaires: la grotte de La Borie del Rey (Lot-et-Garonne). *Gallia Préhistoire* 6, 1–29
- Cravinho, S. & Desse-Berset, N. 2005. Les poissons du Bois-Ragot (Gouex, Vienne). In A. Chollet (ed.), *La grotte du Bois-Ragot à Gouex (Vienne): Magdalénien et Azilien: essais sur les homes et leurs environnements*, 355–71. Paris: Mémoire de la Société préhistorique française 38
- Crégut-Bonnoure, E. 1992. La faune de Mammifères de Chinchon II (Saumane-de-Vaucluse, Vaucluse). *Bulletin Archéologique de Provence* 21, 9–13
- Currant, A.P. 1986. The Lateglacial mammal fauna of Gough's Cave, Cheddar, Somerset. *Proceedings of the University of Bristol Spelaeological Society* 17, 286–304
- Currant, A. P. & Jacobi, R. 2011. The mammal faunas of the British Late Pleistocene. In N.M. Ashton, S.G. Lewis & C.B. Stringer (eds), *The Ancient Human Occupation of Britain*, 181–222. Amsterdam: Elsevier
- Dachary, M. 2008. *Le Magdalénien des Pyrénées occidentales*. Nanterre: Université de Nanterre
- David, S., 1996. La fin du Paléolithique supérieur en Franche-Comté: environnement, cultures, chronologie. *Gallia Préhistoire* 38(1), 111–248
- Davies, W., White, D., Lewis, M. & Stringer, C. 2014. Evaluating the transitional mosaic: frameworks of change from Neanderthals to *Homo sapiens* in eastern Europe. *Quaternary Science Reviews* 118, 211–42
- Dawkins, R. 1982. *The Extended Phenotype*. Oxford: Freeman
- Dawson T.P., Jackson S.T., House J.I., Prentice I.C. & Mace G.M. 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* 332, 53–8
- Deelder, C.L. 1985. *Exposée synoptique des données sue languille, Anguilla Anguilla (Linnaeus 1758)*. Food and Agriculture Organisation (FAO) Synopsis Pêches 80 Revue 1.
- Dods, R. 2003. Wondering the wetland: archaeology through the lens of myth and metaphor in northern Boreal Canada. *Journal of Wetland Archaeology* 3, 17–36
- Duche, G. 1986–7. Première approche de la faune ichtyologique du Niveau 2B du Bois des Brousses, Aniane, Hérault. *Études Quaternaires Languedociennes Cahier* 5, 14–20
- Enloe, J. G. 2006 Geological processes and site structure: Assessing Integrity at a Late Paleolithic open-air site in northern France. *Geoarchaeology* 21, 523–40
- Fiedorczuk, J., Bratlund, B., Kolstrup, E. & Schild, R., 2007. Late Magdalenian feminine flint plaquettes from Poland. *Antiquity* 81(311), 97–105
- Fiore, I., Gala, M. & Tagliacozzo, A. 2004. Ecology and Subsistence Strategies in the Eastern Italian Alps during the Middle Palaeolithic. *International Journal of Osteoarchaeology* 14. 273 – 286.
- Fontana L. 2000. La chasse au renne au Paléolithique supérieur dans le Sud-ouest de la France: nouvelles hypothèses de travail. *Paléo* 12, 141–64
- Fosse, P. 1999. La grande faune mammalienne: remarques préliminaires. In C. Chauchat (ed.), *L'habitat Magdalénien de La Grotte Bourrouilla À Arancou (Pyrénées Atlantiques)*, 98–113. *Gallia Préhistoire* 41
- Gambier, D., Valladas, H., Tisnerat-Laborde, N., Arnold, M. & Bresson, F. 2000. Accelerator mass spectrometry radiocarbon dating of human remains from the Upper Palaeolithic. *Paléo* 12, 201–12
- Garrod, D. 1955. Palaeolithic spear throwers. *Proceedings of the Prehistoric Society* 21, 21–35
- Gill, J.L., Williams, J.W., Jackson, S. T., Donnelly, J.P. & Schellinger, G.C. 2012. Climatic and megaherbivory controls on late-glacial vegetation dynamics: a new, high-resolution, multi-proxy record from Silver Lake, Ohio. *Quaternary Science Reviews* 34, 66–80

- Gleed-Owen, C.P. 1999. The palaeoclimatic and biostratigraphic significance of herpetofaunal remains in the British Quaternary. In P. Andrews & P. Banham (eds), *Late Cenozoic Environments and Hominid Evolution: A tribute to Bill Bishop*, 201–15. London: Geological Society of London
- Graziosi, P. 1960. *Paleolithic Art*. New York: McGraw Hill
- Guthrie, R.D. 2006. *The Nature of Paleolithic Art*. Chicago: University of Chicago Press.
- Häglund, A. & Sjöberg, G. 1999 Effects of beaver dams on the fish fauna of forest streams. *Forest Ecology and Management* 115, 259–66
- Halstead, B.W. 1988. *Poisonous and Venomous Marine Animals of the World*. Princeton: Darwin Press (2 rev. edn)
- Hardy, K., Radini, A. & Buckley, S. 2015. Diet, medicines, raw materials or palaeoenvironments? A broad approach to materials extracted from Palaeolithic dental calculus. Unpublished European Society for Human Evolution Conference Podium Presentation
- Hardy, K., Radini, A., Buckley, S., Sarig, R., Copeland, L., Gopher, A. & Barkai, R. 2016. Dental calculus reveals potential respiratory irritants and ingestion of essential plant-based nutrients at Lower Palaeolithic Qesem Cave Israel. *Quaternary International* 398, 129–35
- Hardy, S. & Buckley, H.M. 2013. Neanderthal self-medication in context. *Antiquity* 87, 873–8
- Harrod, L., Grey, J., McCarthy, T.K. & Morrissey, M. 2005. Stable isotope analyses provide new insights into ecological plasticity in a mixohaline population of European eel. *Oecologia* 144, 673–83
- Hatfield, G. 2004. *Encyclopedia of Folk Medicine: Old World and New World traditions*. Santa Barbara: ABC-CLIO
- Hérisson, D., Locht, J.-L., Vallin, L., Deschodt, L., Antione, P., Auguste, P., Limondin-Lozouet, N., Lefèbvre, S., Hulin, G., Masson, B. & Ghalen, B. 2015. Neandertals' presence during the Eemian Interglacial in north-western Europe: a new site at Waziers (northern France). Unpublished European Society for Human Evolution Conference Podium Presentation
- Hodgson, D. 2003. The biological foundations of Upper Palaeolithic Art: Stimulus, percept and representational imperatives. *Rock Art Research* 20, 3–22
- Hodgson, D. 2014. The significance of the Pech Merle spotted horses. *Arts* 3, 207–12
- Hoek, W.Z. 1997. Patterns of Lateglacial vegetation in the Netherlands. *Eiszeitalter u. Gegenwart* 47, 78–88
- Hurcombe, L. 2014. *Perishable Material Culture in Prehistory: Investigating the missing majority*. London: Routledge
- Isturitz Websites. Musée d'Archeologie Nationale et Domaine, St-Germain-en-Laye. <http://musee-archeologienationale.fr/> and <http://donsmaps.com/isturitz.html> and <http://www.arretetonchar.fr/>
- Izquierdo, E.R. 1992. La ictiofauna musteriense de Cueva Millan (Burgos): consideraciones de índole biológica y cultural contrastadas con ictiocenosis paleolíticas Cantabricas. *Estudios Geológicos* 48, 79–83
- Julien, M. 1982. *Les Harpons Magdaléniens*. Paris: Editions du Centre national de la recherche scientifique
- Julien, M. 1995. Harpons Magdaléniens. In A. Averbouth, C. Bellier & A. Billambozet (eds), *Fiches Typologiques de L'industrie Osseuse Préhistorique. Cahier VII: Éléments Barbelés et Aparentes*, 83–99. Treignes: Centre d'Etudes et de Documentation Aicheoologiques (CEDARC)
- Keffer, W.J. & Welsh, A.E. 1936. Hemolytic and toxic properties of certain serums. *Mendel Bulletin* 8, 76–80
- Kettle, A. J., Heinrich, D., Barrett, J. H. Benecke, N. & Locker, A. 2008. Past distribution of European freshwater eel from archaeological and palaeontologist evidence. *Quaternary Science Reviews* 27, 1309–34
- Kitchener, A. 2001. *Beavers*. Stowmarket: Whittet Books
- Kuntz, D. & Costamagno, S. 2011. Relationship between reindeer and man in southwestern France during the Magdalenian. *Quaternary International* 238, 12–24
- Kuratko, L.N., Cernkovitch Barertt, E., Nelson, E.R. & Salem, N. 2013. The relationship of docosahexaenoic acid (DHA) with learning and behaviour in healthy children: A review. *Nutrients* 5, 2777–810
- Laland, K.N. & O'Brien, M. J. 2010 Niche construction theory and archaeology. *Journal of Archaeological Method & Theory* 17, 303–22
- Lane, P. 2014. Hunter-gatherer-fishers, ethnoarchaeology and analogical reasoning. In V. Cummings, P. Jordan & M. Zvelebil (eds), *Oxford Handbook of the Archaeology and Anthropology of Hunter-Gatherers*, 104–50. Oxford, Oxford University Press
- Langley, M.C. 2013. A newly discovered horse engraving from La Madeleine (Dordogne), France. *Proceedings of the Prehistoric Society* 79, 377–81
- Langley, M. 2014. Magdalenian antler projectile point design: Determining original form for uni- and bilaterally barbed points. *Journal of Archaeological Science* 44, 104–16
- Lebreton, L., Moigne, A.-M., Filoux, A. & Perrenoud, C. 2017. A specific small game exploitation for Lower Paleolithic: The beaver (*Castor fiber*) exploitation at the Caune de l'Arago (Pyrénées-Orientales, France). *Journal of Archaeological Science Reports* 11, 53–8
- Le Gall, O. 1999. *Ichtyophagie et pe`ches prehistoriques. Quelques donne'es de l'Europe occidentale*. Unpublished Ph.D. Thesis, L'Université Bordeaux I
- Leroi-Gourhan, A. 1968. *The Art of Prehistoric Man in Europe*. London: Thames & Hudson
- Leroi-Gourhan, A. & Allain, J. 1998. *Lascaux inconnu*. Paris: CNRS
- Lespez, L., Viel, V., Rollet, A.J. & Delahaye, D. 2015. The anthropogenic nature of present-day low energy rivers in western France and implications for current restoration projects. *Geomorphology* 251, 64–76
- Lévi-Strauss, C. 1964. *The Raw and the Cooked*. Paris: Plon
- Lewis, B. 2009. *Hunting in Britain from the Ice Age to the Present*. Stroud: History Press.
- Lewontin, R. C. 2000. *The Triple Helix: Gene, organisms and environment*. Cambridge MA: Harvard University Press
- Liarsou, A. 2014. Zones refuges glaciaires et processus de recolonisation tardiglaciaire et holocene du castor (*Castor fiber* L.) en Europe: aperçu synthétique des données archéozoologiques. *HAL Archives-Ouvert*, 1–24.
- Lottter, A.F., Heiri, O., Brooks, S., van Leeuwen, J.F.N., Eicher, U. & Ammann, B. 2012. Rapid summer temperature change during Termination 1a: high resolution multi-proxy climate reconstructions from Gerzensee (Switzerland). *Quaternary Science Reviews* 36, 103–13
- MacCurdy, G.G. 1924. The field of Paleolithic art. *American Anthropologist* 26, 27–49

- Madden, J.R., Dingle, C., Isden, J., Sparfield, J., Goldizan, A.W. & Endler, J.A. 2012. Male spotted bowerbirds propagate fruit for use in their sexual display. *Current Biology* 22, R264–5
- Maier, A. 2015. *The Central European Magdalenian*. Dordrecht: Springer
- Marr, M. 2016. Radiocarbon dating of European beaver (*Castor fiber* L. 1958) from Gough's Cave provides evidence of population persistence over the Younger Dryas in Britain. *Proceedings of the University of Bristol Speleological Society* 27, 105–8
- Marshack, A. 1972. *The Roots of Civilisation: The cognitive beginnings of man's first art, symbol and notation*. New York: McGraw Hill
- Mas D'Azil Website 2012. references: <http://anetcha-parisienne.blogspot.com.au/2012/09/en-passant-par-saint-germain-en-laye.html> and <http://donsmaps.com/masdazil.html>
- Meentemeyer, R.K. & Butler, D.R. 1999. Hydrogeomorphic effects of beaver dams in Glacier National Park, Montana. *Physical Geography* 20, 436–46
- Mihlbachler, M.C., Rivals F., Solounias N. & Semprebon G. M. 2011. Dietary change and evolution of horses in North America. *Science* 331, 1178–81
- Miller, R. 2012. Mapping the expansion of the Northwest Magdalenian. *Quaternary International* 273, 209–30
- Musil, R. 2000 Hunting in Central Europe at the end of the Last Glacial. *Anthropologie et Préhistoire* 111, 233–36
- de Nadaillac, A. 1887. Mœurs et monuments des peuples pré-historiques. *Comptes-rendus des séances de l'Académie des Inscriptions et Belles-Lettres, Année 1887*, 31, 42–9
- Naiman, R.J., Johnston, C.A. & Kelly, J.C. 1988. Alteration of North American streams by beaver. *Bioscience* 38, 753–62
- Neer, W. van, Wouters, W. & Germonpre, M. 2007. Fish remains from three Upper Palaeolithic cave deposits in southern Belgium. *Anthropologica et Præhistorica* 118, 5–22
- Nitecki, M.H. & Nitecki D.V. (eds) 1987. *Evolution of Human Hunting*. New York: Plenum Press
- Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. 2003. *Niche Construction. The Neglected Process in Evolution*. Princeton: Princeton University Press
- Odling-Smee, J., Erwin, D.H., Palkovacs, E.P., Feldman, M.W. & Laland, K.N. 2013. Niche construction theory: A practical guide for ecologists. *Quarterly Review of Biology* 88, 3–28
- Osborn, H.F. 1915. *Men of the Old Stone Age: Their environment, life and art*. New York: Charles Scribner's Sons
- Osgood, C. 1940. *Ingalik Material Culture*. New Haven: Yale University Publications in Anthropology 22
- Pacher, M. 2006. Large mammal remains from the Mladec Caves and their contribution to site formation processes. In M. Teschler-Nicola (ed.), *Early Modern Humans at the Moravian Gate: The Mladec Caves and their Remains*, 99–148. Dordrecht: Springer
- Pante, M.C., Blumenschine, R.J., Capaldo, S.D., & Scott, R.S. 2012. Validation of bone surface modification models for inferring hominin and carnivore feeding interactions, with reapplication to FLK 22, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 63, 395–407
- Pastre, J.-F., Limondin-Lozouet, N., Leroyer, C., Ponel, P. & Fontugne, M. 2003. River system evolution and environmental changes during the Lateglacial in the Paris Basin (France). *Quaternary Science Reviews* 22, 2177 – 2188.
- Pêcheurs, A. D. E. S., Flandin, D. E. L. a B., Moncel, M., Daujeard, C., Cregut-bonnoure, É., Boulbes, N., Puaud, S., Debard, É., Bailon, S., Desclaux, E., Escude, É., Roger, T. & Dubar, M., 2010. Nouvelles données sur les occupations humaines du début du Pléistocène supérieur de la moyenne vallée du Rhône (France). Les sites de l'Abri des Pêcheurs, de la Baume Flandin, de l'Abri du Maras et de la Grotte du Figuier (Ardèche). *Quaternaire* 21(4), 385–411
- Petillon, J-M. 2008. What are these barbs for? Preliminary reflections on the function of the Upper Magdalenian barbed weapon tips/Des barbelures pour quoi faire? Reflexions préliminaires sur la fonction des pointes barbeles du Magdalénien supérieur. *Palethnologie* 1, 66–97/69–102 <halshs-00403708>
- Peyrona, O., Be'geota T, C., Brewerb S., Heiric, O., Magnya, M., Milleta, L., Ruffaldia, P., Van Campod, E. & Yue, G. 2005. Late-Glacial climatic changes in Eastern France (Lake Lautrey) from pollen, lake-levels, and chironomids. *Quaternary Research* 64, 197–211
- Pfeiler, E. 1986. Towards and explanation of the developmental strategy in leptocephalous larvae of marine teleost fishes. *Environmental Biology of Fishes* 15, 3–13
- Piette, E. 1907. *L'Art pendant l'âge du renne*. Paris
- Pigaud, R. 2002. Le Cheval dans l'Art paléolithique: observé, disséqué ... interprété. In L. Bodson (ed.), *D'os, d'images et de mots. Contribution à la réflexion sur les sources de l'histoire des connaissances zoologiques*, 3–34. Liège: Université de Liège
- Pion, G., 2009. *La fin du Paléolithique supérieur dans les alpes du nord françaises et le Jura méridional. Approches culturelles et environnementales*, 255–270. Paris: Société Préhistoriques Française
- Ponel, P. & Coope, G.R. 1990. Lateglacial and eearly Flandrian coleoptera from La Taphanel, Massif Central, France : Climatic and ecological implications. *Journal of Quaternary Science* 5, 235–49
- Power, R.C., Salazar-García, D.C., Straus, L.G., González Morales, M.R. & Henry, A.G. 2015. Microremains from El Mirón Cave human dental calculus suggest a mixed plant-animal subsistence economy during the Magdalenian in Northern Iberia, *Journal of Archaeological Science* 60, 39–46
- Pozzi E. 2004. *Les Magdaléniens. Art, civilisations, modes de vie, environnements*. Grenoble: Millon
- Prosek, J. 2011. *Eels: An exploration from New Zealand to the Sargasso of the Worlds most mysterious fish*. New York: Harper Collins
- Radini, A., Buckley, S., Rosas, A., Estalrich, A., de la Rasilla, M., Hardy, K. **in press**. Neanderthals and trees: Non-edible conifer fibres found in Neanderthal dental calculus suggests extra-masticatory activity. *Antiquity*
- Rhind, P. & Jones, B. 2003. The vegetation history of Snowdonia since the Lateglacial Period. *Field Studies* 10, 539–52
- Rice, P.C. & Paterson, A.L. 1996. Bone art in the Upper Palaeolithic: regional, temporal, and art classcomparisons. *Cross-Cultural Research* 30, 211–42
- Righton, D. & Roberts, M. 2014. Eels and people in the United Kingdom. In Tsukamoto & Kuroko (eds) 2014, 1–12
- Roach, N.T., Venkadesan, M., Rainbow, M.J. & Lieberman, D.E. 2013. Elastic energy storage in the shoulder and the evolution of high-speed throwing in *Homo*. *Nature* 498, 483–7

- Roberts, M.B. & Parfitt, S.A. 1999. *Boxgrove. A Middle Pleistocene hominid site at Earham Quarry, Boxgrove, West Sussex*. London: English Heritage Archaeological Report 17
- Román, D. & Villaverde, V. 2012. The Magdalenian harpoons from the Iberian Mediterranean, base don pieces from Cova de les Cendres (Teulada-Moraire, Valencia region). *Quaternary International* 272–3, 33–41
- Roselló, E., Morales, A., 1995. Ictiofauna. In Cacho, C., Fumanal, M.P., López, P., López, J.A., Pérez Ripoll, M., Martínez Valle, R., Uzquiano, P., Arnanz, A., Sánchez Marco, A., Sevilla, P., Morales, A., Roselló, E., Garralda, M.D., García-Carrillo, M. (eds), *El Tossal de la Roca (Vall d'Alcalà, Alicante). Reconstrucció'n paleoambiental y cultural de la transició'n del Tardiglaciari al Holoceno Inicial*, 63–5. Alcoi: Recerques del Museu d'Alcoi 4
- Salazar-García, D.C. Power, R.C. Sanchis Serra, A. Walker, M.J. & Henry, A.G. 2013. Neanderthal diets in central and southeastern Mediterranean Iberia. *Quaternary International* 318, 3–18
- Sato, M. 1917. Blood serum of the eel. *Nippon Biseibutsugakukai Zasshi* 5, 473–000
- Schmidt, E.J. 1922. The breeding places of the eel. *Philosophical Transactions of the Royal Society* 211, 179–208
- Schwartz, J. & Tattersall, I. 2006. Foreward, in M. Teschler-Nicola (ed.), *Early Modern Humans at the Moravian Gate: Mladec Caves and their Remains*, xi–xiii. Vienna/New York: Springer.
- Shennan, S. 2001 Demography and cultural innovation: A model and its implications for the emergence of modern human culture. *Cambridge Archaeological Journal* 11, 5–16
- Shillito, L.M. 2013. Grains of truth or transparent blindfolds? A review of current debates in archaeological phytolith analysis. *Vegetation History & Archaeobotany* 22, 71–82
- Sieveling, A. 1987. *A Catalogue of Palaeolithic art in the British Museum*. London, British Museum Publications
- Simões de Abreu & Bednarik, R. G. 2000. Fariseu rock art not archaeologically dated. *Rock Art Research* 17, 65–8
- Sinha, V.R. & Jones, J.W. 1975. *The European Freshwater Eel*. Liverpool: Liverpool University Press
- Sistiaga, A., Mallol C., Galván, B. & Summons, R.E. 2014. The Neanderthal meal: A new perspective using faecal biomarkers. *PLoS ONE* 9, e101045
- Smart, D.J.Q. 2003. *Later Mesolithic Fishing Strategies and Practices in Denmark*. Oxford: British Archaeological Report S1119
- Smith, B.D. 2007. Nice construction and the behavioural context of plant and animal domestication. *Evolutionary Anthropology* 16, 188–99
- Soffer O., Adovasio, J.M. & Hyland, D.C. 2000a. The 'Venus' figurines, textile, basketry, gender, and status in the Upper Palaeolithic. *Current Anthropology* 41(4), 511–37
- Soffer, O., Adovasio, J.M., Illingworth, J.S., Amirkhanov, H.A., Prasvlov, N.D. & Street, M., 2000b. Palaeolithic Perishables made Permanent. *Antiquity* 74, 812–21
- Sommer, R. & Beneck, N. 2004. Late- and Post-Glacial history of mustelids. *Mammal Review* 34, 249–84
- Speth, J.D. 1991. Nutritional constraints and Lateglacial adaptive transformations: the importance of non-protein energy sources. In Barton *et al.* (eds) 1991, 169–78
- Stachurska, A.M. 1999. Inheritance of primitive markings in horses. *Journal of Animal Breeding and Genetics* 116, 29–38
- Stapert, D. & Street, M. 1997. High resolution or optimum resolution? Spatial analysis of the Federmesser site at Andernach, Germany. *World Archaeology* 29, 172–94
- Stevens, R.E., O'Connell, T.C., Hedges, R.E.M. & Street, M., 2009. Radiocarbon and stable isotope investigations at the Central Rhineland sites of Gönnersdorf and Andernach-Martinsberg, Germany. *Journal of Human Evolution* 57(2), 131–48
- Stiner, M.C. 2002. Carnivory, coevolution, and the geographic spread of the genus *Homo*. *Journal of Archaeological Research* 10, 1–63
- Stiner, M. Barkai, R. & Gopher, A. 2009. Cooperative hunting and meat sharing 400–200 kya at Qesem Cave, Israel. *Proceedings of the National Academy of Sciences of the USA* 106(32), 13207–12
- Straus, G., 1988. L'abri Dufauré et la Falaise du Pastou dans le système adaptatif régional des Pyrénées au Magdalénien. In *Colloque de Chancelade*, 335–343. **Place of publication: publisher**
- Street, M., Gelhausen, F., Grimm, S., Moseler, F., Niven, L., Sensburg, M., Turner, E., Wenzel, S. & Jöris, O. 2006. L'occupation du bassin de Neuwied (Rhénanie centrale, Allemagne) par les Magdaléniens et les groupes à Federmesser (aziliens). *Bulletin de La Société Préhistorique Française* 103(4), 753–80
- Svoboda, J. 2001. Mladec and other caves in the Middle Danube region: early modern humans, late Neandertals, and projectiles. In J Zilhão, T. Aubry & A.F. Carvalho (eds), *Les premiers homes modernes de la Peninsule Iberique*, 45–60. Lisbon: Portuguese Institute of Archaeology Press
- Tesch, F.W. 2003. *The Eel*. Oxford: Blackwell (5 edn)
- Thonicke, K., Prentice, I.C. & Hewitt, C. 2005. Modeling glacial-interglacial changes in global fire regimes and trace gas emissions. *Global Biogeochem. Cycles* 19, GB3008, 1–10
- Tsukamoto, K. & Kuroki, M. 2014. *Eels and Humans*. Tokyo: Springer
- Turner, E. 2006. Results of a recent analysis of horse remains dating to the Magdalenian period at Solutre, France. In M. Mashkour (ed.), *Equids in Time and Space*, 70–89. Oxford: Oxbow Books
- Tyldesley, J.A. & Bahn, P.G. 1983. Use of plants in the European Palaeolithic: A review of the evidence. *Quaternary Science Reviews* 2, 53–81
- Urban, B. & Bigga, G., 2015. Environmental reconstruction and biostratigraphy of late Middle Pleistocene lakeshore deposits at Schöningen. *Journal of Human Evolution* 89, 57–70
- Vøllestad, L. A. 1992. Geographic variation in age and length at metamorphosis of maturing European eel: environmental effects and phenotypic plasticity. *Journal of Animal Ecology* 61, 41–8
- Walker, M.J.C. *et al.* 2009. Formal definition and dating of the GSSP (Global Stratotype Section and Point) for the base of the Holocene using the Greenland NGRIP ice core, and selected auxiliary records. *Journal of Quaternary Science* 24, 3–17
- Walker, M.J.C. *et al.* 2012. Formal subdivision of the Holocene series/epoch: A discussion paper by a working group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommittee on Quaternary Stratigraphy (International Commission on Stratigraphy). *Journal of Quaternary Science* 24, 3–17
- Westbrook, C.J., Cooper, D.J. & Baker, B.W. 2011. Beaver assisted river valley formation. *River Research and Applications* 27, 247–56

- Wheeler, A. 1969. *Fishes of the British Isles and North West Europe*. London: Macmillan
- Xiang M, Alfvén G, Blennow M, Trygg M, & Zetterström R. 2000. Long-chain polyunsaturated fatty acids in human milk and brain growth during early infancy. *Acta Paediatrica* 89, 142–47
- Yoshida, M., Sone, S. & Shiomi, K. 2008. Purification and characterization of a proteinaceous toxin from the serum of Japanese eel *Anguilla japonica*. *Protein Journal* 27, 450–54
- Zhilin, M.G. 2014. Early Mesolithic hunting and fishing in Central Russia on wetland sites. *Journal of Wetland Archaeology* 14, 91–105
- Zubrow, E. 2010. Archaeology of equality: Magdalenian economy. In E.B.W. Zubrow, F. Audouze & J.G. Enloe (eds), *The Magdalenian Household Unraveling Domesticity*, 109–30. New York: SUNY Series, Institute for European and Mediterranean Archaeology Distinguished Monograph Series
- Zvelebil, M. 2008. Innovating hunter-gatherers: The Mesolithic in the Baltic. In G. Bailey (ed.), *Mesolithic Europe*, 18–59. Cambridge: Cambridge University Press

[H1]RÉSUMÉ

[10P] *Anguilles, castors et chevaux: Construction de niche humaine dans la deuxième partie du paléolithique supérieur européen*, de Antony G. Brown, Laura S. Basell et Rebecca Farbstein

Cet article examine les interactions entre les divers occupants de niches riveraines dans l'Europe du nord-ouest durant la deuxième partie du paléolithique supérieur final utilisant à la fois des données écologiques et archéologiques. On argumente que l'étude à la fois des récents vestiges de glaciation et de l'autécologie des anguilles, castors et chevaux donne du poids à une réinterprétation de certains célèbres, mais énigmatiques, panneaux d'art mobilier magdalénien comme représentation de pêche à l'anguille, au côté de l'exploitation de chevaux et de castors dans des habitats riverains perturbés. On propose, de plus, que ceci constitue une niche humaine co-construite en termes d'écologie, de nutrition et de symbole, qui était aussi particulièrement propice au bien-être et à l'avancement social en ce temps et lieu.

ZUSSAMENFASSUNG

Aale, Biber und Pferde: Die Bildung menschlicher Nischen im europäischen Späten Jungpaläolithikum, von Antony G. Brown, Laura S. Basell und Rebecca Farbstein

Dieser Beitrag untersucht Interaktionen zwischen den verschiedenen Nutzern ökologischer Nischen in Fließgewässerräumen in Nordwesteuropa im Späten Jungpaläolithikum auf Basis von sowohl ökologischen als auch archäologischen Daten. Es wird argumentiert, dass eine Berücksichtigung der Datenlage zum Spätglazial einerseits und der Autökologie von Aalen, Bibern und Pferden andererseits die Grundlagen für eine neue Interpretation einiger berühmter, aber rätselhafter Bilderreihen mobiler magdalenienszeitlicher Kunst liefert als Darstellungen von Aalfischerei sowie Ausbeutung von Pferden und Bibern in gestörten flussnahen Habitaten. Weiterhin wird erwogen, dass dies eine auch menschlich erzeugte Nische im ökologischen, diätischen und symbolischen Sinne war, die zudem besonders vorteilhaft für das menschliche Wohlergehen und die soziale Entwicklung zu dieser Zeit und in diesem Raum war.

RESUMEN

Anguilas, castores y caballos: construcciones de los nichos humanos en el Paleolítico Superior Final, por Antony G. Brown, Laura S. Basell y Rebecca Farbstein

En este artículo se examinan las interacciones entre los ocupantes de los nichos ribereños en el noroeste de Europa durante el Paleolítico Superior final, a partir de los datos ecológicos y arqueológicos. La documentación durante el último glacial y la ecología de poblaciones de algunas especies como la anguila, el castor y el caballo apoyan una reinterpretación de algunos famosos pero enigmáticos restos de arte mueble magdaleniense tales como representaciones de la pesca de la anguila y la explotación de caballos y castores en hábitats ribereños alterados. Se sugiere además que esto supone un nicho construido por parte de los seres humanos en términos ecológicos, nutricionales y simbólicos, lo que fue particularmente ventajoso para el bienestar humano y su desarrollo social en ese momento y entorno.

Fig. 1. Magdalenian Europe with ecological, palaeontological, and Magdalenian art sites mentioned in the text. Stars: sites with art reproduced in this paper; solid circles: other Magdalenian sites mentioned in the text

Fig. 2 A poke pole being used to flush eels out for filming (photo courtesy of the Monkeyface News)

Fig. 3 A scene of horse head eeling from the 1979 adaptation of *The Tin Drum* by Gunter Grass directed by Volker Schlöndorff and produced by Jadran Films (Reproduction by permission of Jadran Films, Croatia)

Fig. 4. A Maori eel-weir on the outlet stream of Horowhenua lake New Zealand (above) and eel killing baton (*patu tuna*) and eel spears (*matarau*) (below) (by permission from Museum of New Zealand Collections. Wweir photographer Leslie Adkin 1925, gift of the G.L. Adkin family estate 1964)

Fig. 5. 'Snake or eel, man and two horse heads' from Abri La Madelaine redrawn from Marshack (1972) (redrawn and adapted from original © MNP Les Eyzies – Dist.RMN - cliché Ph. Jugie)

Fig. 6. Engraving on a *bâton de commandement* from Grotte ds Montgaudiet from de Nadaillac (1887) (Creative Commons licence)

- Fig. 7. 'horses head with herbage' from Grotte du Mas d'Azil, adapted from Tyldesley & Bahn (1983) (copyright: Elsevier)
- Fig. 8. Three panels from Lortet. Magdalenian. From Antropomorfos en la Cueva de los Casaresal Website, (<http://quintadimension.blogcindario.com/2008/09/00019-antropomorfos-en-la-cueva-de-los-casares.html>) (Creative Commons licence)
- Fig. 9. engraved bone of an anthropomorph entitled 'The sorcerer of La Madeleine' from Abri La Madeleine (reproduced by permission of the Musée Les-Eyzies-de-Tayac. © MNP Les Eyzies – Dist.RMN - cliché Ph. Jugie)
- Fig. 10. Schematic representation of ecological relationships between humans, beaver, eels and horses in the European Late Upper Palaeolithic

¹Palaeoenvironmental Laboratory University of Southampton (PLUS), Shackleton Building, Highfields Campus, Southampton SO17 1BJ UK. Email: Tony.Brown@soton.ac.uk

²School of Natural & Built Environment, Queen's University Belfast, University Road, Belfast, BT7 1NN, Northern Ireland

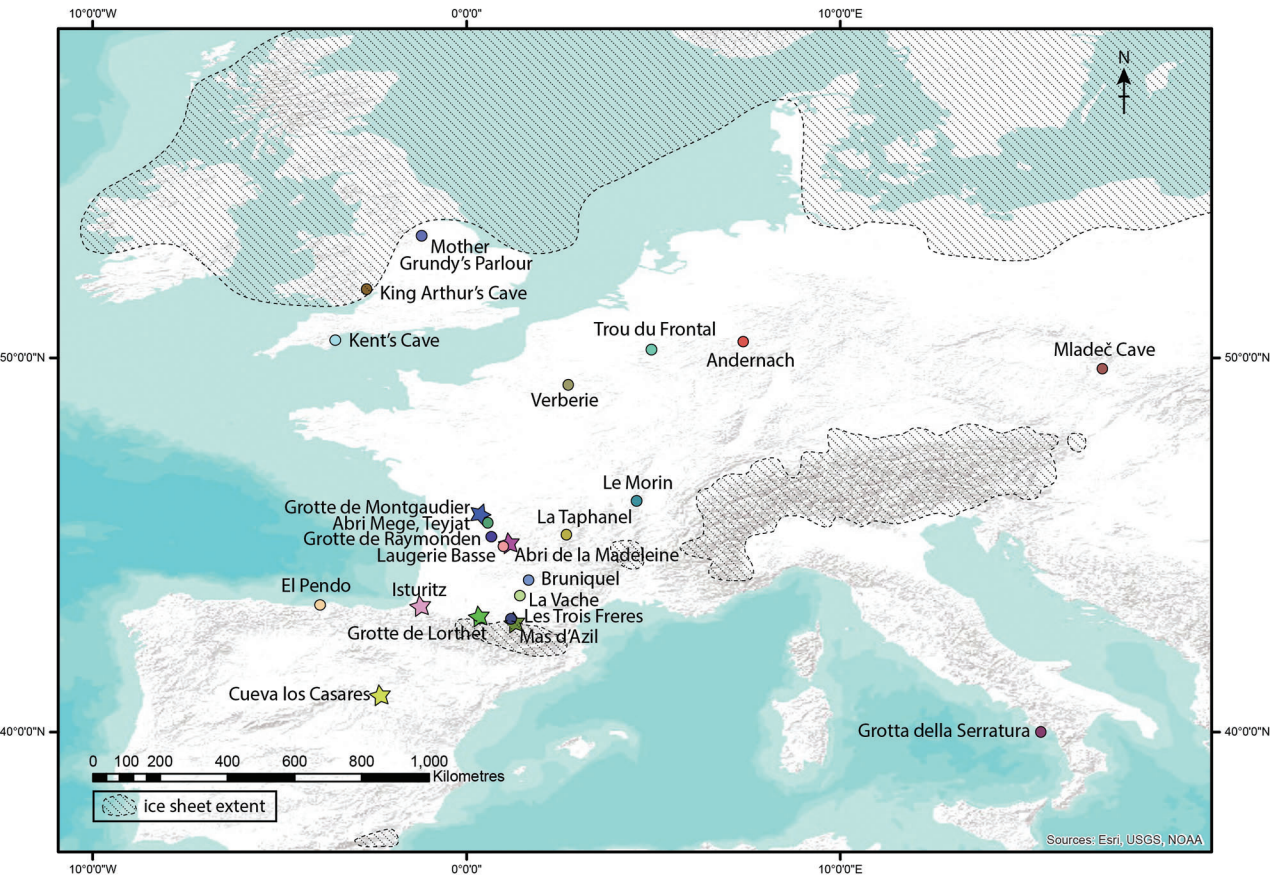
³Department of Archaeology, University of Southampton, Avenue Campus, Southampton SO17 1BJ

running header

A. Brown. EELS, BEAVERS, HORSES: HUMAN NICHE CONSTRUCTION, EUROPEAN LUP

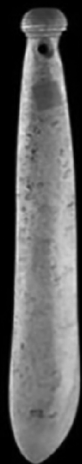
TABLE 1: FOSSIL EVIDENCE OF EEL & BEAVER PRESENCE IN MAGDALENIAN & FEDERMESSER WESTERN EUROPE

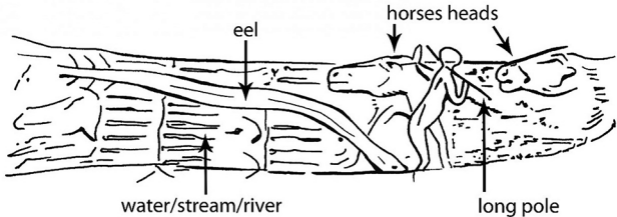
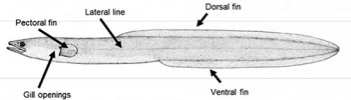
	<i>Site</i>	<i>Evidence</i>	<i>Date(s)</i>	<i>References</i>
<i>Eel</i>	Les Peyrugue S, Atlantic, France	Vertebrae	29,650–31,360 cal BP	Le Gall 1999
	Bois des Brousses, Aniane, Hérault, France	Vertebrae	Middle Magdalenian c. 18,500 cal BP	Duche 1986–7
	Tossal de la Rocca, Alicante, Spain (668 m altitude)	Vertebrae	17,020–19,540 cal BP	Roselló & Morales 1995
	Bois Ragot (Level 5), Atlantic, France	vertebrae	Final Magdalenian Younger Dryas II ancient 14,150 cal BP	Cravinho & Desse-Berset 2005
	Mladec, Czech Republic	Perforated beaver incisors	Aurignacian	Pacher 2006
<i>Beaver</i>	Les Hoteaux, Mas d’Azil, France	Bones with human burial	Magdalenian	Burkitt 1921
		Bone	Magdalenian, Azilian levels,	Osborn 1915
	Le Morin rock-shelter, Gironde, France	Bones with human modifications in association with human occupation	Magdalenian	Boudadi-Maligne <i>et al.</i> 2012
	Grottes des Hoteaux, Rossillon, France	Bones possibly associated with a burial?	Magdalenian	Burkitt 1921
	Hohlen Stein, Westphalia, Germany	Bone	Middle Magdalenian	Clark 1936
	Nørre-Lyngby, Denmark	Bone	Middle-Late Magdalenian	Aaris-Sorensen 2009
	Balcarova skala Cave	Bone from fireplace 2	Magdalenian	Musil 2000
	Moravian Karst, Czech Republic			
	Les Pecheurs, Casteljau, France	Bone (faunal list)	Mousterian & Upper Palaeolithic	Pêcheurs <i>et al.</i> 2010
	Wilczyce, Poland	bone	c. 15,000 cal BP Late Magdalenian	Fiedorczukt <i>et al.</i> 2007
	Grotte de la Borie del Rey, France	Bone (faunal list)	Magdalenian	Couloonges 1963
	Grotte d’Arlay, France	Bone (faunal list)	Magdalenian	David 1996
	La Grotte du Rond du Barry, France	Bone (faunal list)	Magdalenian	Poulain 1972; Liarsou 2014
	La Grotte de Jeannue à Rebeuville, France	Bone (faunal list)	Magdalenian	Poulain 1976; Liarsou 2014
	La Grotte du Bourrouilla, France	Bone (faunal list)	Magdalenian	Fosse 1999; Dachary 2008; Liarsou 2014
	Chinchon I, France	Bone (faunal list)	Magdalenian	Brochier & Livaxhe 1978
	Chinchon II, France	Bone (faunal list)	Magdalenian	Crégut-Bonnoure 1992
	Grotte des Balmes de Glos, France	2 fragments of scapula (faunal list)	Magdalenian final/Azilien	Bocquet 1969; Pion 2009
	L’Abri Dufaure, France	Bone (faunal list)	Magdalenian & Azillian	Straus 1988
	Gough’s Cave, Cheddar, UK	bone	12,386–11836 & 11989–11,405 cal BP	Currant 1986
	Miesenheim II, Germany	Bone (faunal list)	Federmesser	Bosinski 1979; 1983 after Barton <i>et al.</i> 1991
	Kettig, Germany	Bone (faunal list)	Federmesser	Street <i>et al.</i> 2006
	Niederbieber, Germany	Bone (faunal list)	Federmesser	Street <i>et al.</i> 2006

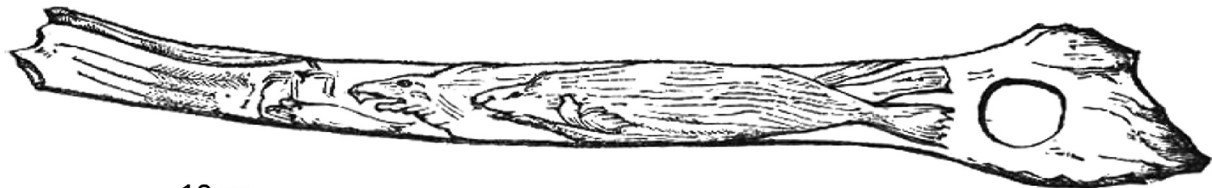




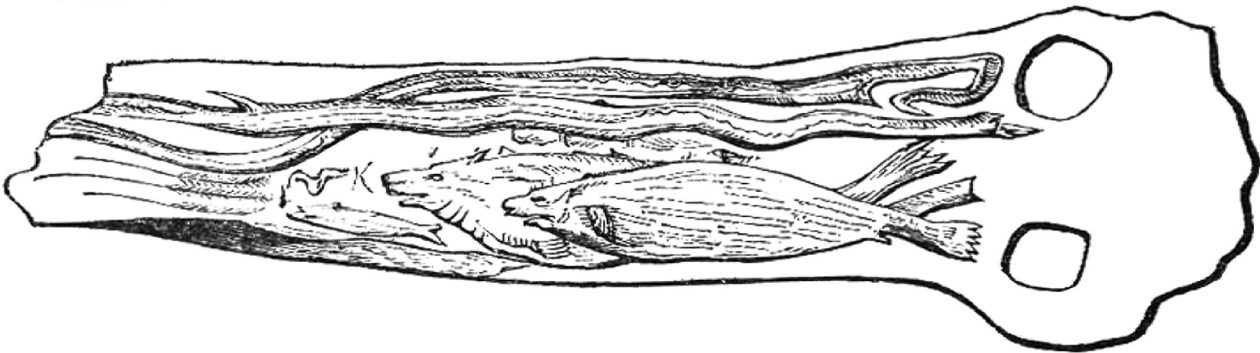


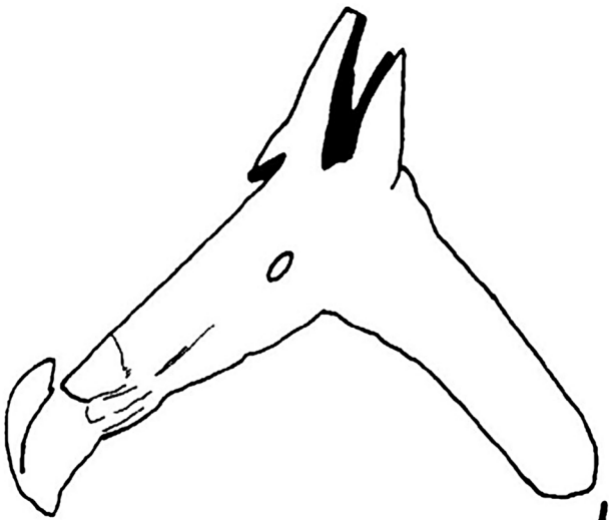






10 cm









Magdalenian riverine corridor

