



# Being-with other predators: Cultural negotiations of Neanderthal-carnivore relationships in Late Pleistocene Europe

Shumon T. Hussain<sup>a,\*</sup>, Marcel Weiss<sup>b</sup>, Trine Kellberg Nielsen<sup>a</sup>

<sup>a</sup> Department of Archaeology and Heritage Studies, Aarhus University, Moesgård Allé 20, 8270 Højbjerg, Denmark

<sup>b</sup> Institut für Ur- und Frühgeschichte, Friedrich-Alexander-Universität Erlangen-Nürnberg, Kochstr. 4/18, 91054 Erlangen, Germany

## ARTICLE INFO

### Keywords:

Human evolution  
Middle Paleolithic  
Neanderthals  
Human-animal interaction  
Multispecies archaeology  
Animal studies  
Palaeoenvironmental humanities  
Sympatry

## ABSTRACT

Late Pleistocene hominins co-evolved with non-analogue assemblages of carnivores and carnivorous omnivores. Although previous work has carefully examined the ecological and adaptive significance of living in such carnivore-saturated environments, surprisingly little attention has been paid to the social and cultural consequences of being-with, and adapting to, other charismatic predators and keystone carnivores. Focusing on Neanderthal populations in Western Eurasia, this paper draws together mounting archaeological evidence that suggests that some Late Pleistocene hominins devised specific behavioral strategies to negotiate their place within the vibrant carnivore guilds of their time. We build on integrative multispecies theory and broader reconceptualizations of human-nature relations to argue that otherwise puzzling evidence for purported 'symbolic' behavior among Neanderthals can compellingly be re-synthesized with their ecology, settlement organization and lifeworld phenomenology. This re-framing of Neanderthal lifeways in the larger context of startling carnivore environments reveals that these hominins likely developed intimate, culturally mediated, and hence varied, bonds with raptor, hyena and bear others, rather than merely competing with them for resources, space and survival. This redressing of human-carnivore relations in the Middle Paleolithic yields important challenges for current narratives on evolving multispecies systems in the Late Pleistocene, complicating our understanding of Late Quaternary megafaunal extinctions and the roles of hominins in these processes.

## 1. Introduction

Both historically and cross-culturally, relationships between humans and other carnivores are often contentious, ambivalent and tension-ridden affairs (Kellert et al. 1996; Campmans 2017; Lamb et al. 2020), yet they similarly rank among the most culturally vigorous and materially generative human-animal interfaces documented by ecologists (Monsarrat and Kerley 2018; Sommerville 2021; Clark et al. 2021), historians (Gade 2006; Zehnle 2015; Widlok 2018), anthropologists (Barsh and Marlor 2003; Rival 2012; Baynes-Rock 2015a) and archaeologists alike (Hahn 1986; Mithen 1999; Clottes and Azéma 2005; Germonpré and Hämaläinen 2007; Betts et al. 2015; Poole 2015; Porr 2015; Hussain and Floss 2015; Costamagno et al. 2018a). Carnivore assemblages and ecological communities of the deep past were extremely diverse and probably considerably enriched in terms of species count and biomass contribution when compared to modern-day carnivore-bearing environments (Turner 1990, 1995; Van Valkenburgh et al. 2016; Galetti et al. 2018; Faith et al. 2019; Stanton et al.

2020). In many parts of the world including Europe, carnivore assemblages were strongly impacted by Late Quaternary extinction trajectories (Stuart and Lister 2007; Malhi et al. 2016; Galetti et al. 2018), putting a final nail to the coffin of most large-bodied carnivores and so-called mega-carnivores that are a hallmark of Pleistocene animal ecologies (Faith et al. 2019). The Late Pleistocene in particular has seen substantial turnover in carnivore community dynamics and composition and documents the extinction of some notable carnivore others (Turner 1985), such as various hyena species with whom hominins in Europe and elsewhere have co-evolved and shared the environment for many millennia (Turner et al. 2008). Some scholars have argued that Eurasian Neanderthals in particular are to be understood as an integral part of situated carnivore ecologies and their associated predator-prey interlinkages, whose gradual disappearance in the second part of the Late Pleistocene may have consequently precipitated the eventual demise of the Neanderthal phenotype at the end of MIS 3 (Estévez 2004; Stewart 2005, 2007).

Previous work has tried to address the importance of Pleistocene

\* Corresponding author.

E-mail address: [s.t.hussain@cas.au.dk](mailto:s.t.hussain@cas.au.dk) (S.T. Hussain).

<https://doi.org/10.1016/j.jaa.2022.101409>

Received 26 August 2021; Received in revised form 14 January 2022;

Available online 1 April 2022

0278-4165/© 2022 The Author(s). Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

hominin-carnivore interactions from the perspective of subsistence behavior (Kindler 2012; Wojtal et al. 2020), competitive exclusion/niche partitioning (Stiner 2002, 2004, 2012; Dusseldorp 2011, 2013; Enloe 2012; Churchill 2014; Orbach and Yeshurun 2019), and energetics or interspecies conflict (Shipman 1984; Binford et al. 1988; Blumenshine 1987; Selvaggio 1994; Kruuk 2002; Turner et al. 2013; Camarós et al. 2016; Domínguez-Rodrigo and Pickering 2017), mostly within the framework of ‘hard’ ecology approaches, including *Human Behavioral Ecology* and generalized Neo-Darwinian evolutionary theory (see also García and Virgós 2007). Even though some of this scholarship acknowledges the potential social significance of the carnivore environment for Neanderthals and other Late Pleistocene hominins (e.g., Wojtal et al. 2020), there is hardly any specific, let alone substantial, engagement with the cultural and material consequences of co-inhabiting environments with ‘charismatic’ carnivore others (sensu Lorimer 2007; Ducarme et al. 2013), for example in terms of interspecies sympatry (but see Brantingham 1998; White and Pettitt 2011: 51; Jimenez et al. 2021), landscape learning and sharing, home-making/neighborhood, attuned cognition and perception, or extended, ‘more-than-human’ kinship – common axes of investigation in multispecies studies. Foregoing scholarship on hominin-carnivore relations, in other words, has overwhelmingly focused on questions of survival, niche coordination and environmental adaptation, largely ignoring, or glossing over, the *phenomenological* implications of living-with and engaging-with powerful carnivore others. At least in part, the focus on die-hard issues of subsistence, and especially *competition* with other carnivores, remains a living legacy of Binford’s (1989) *New Archaeology*-founding critique on Neanderthal hunting prowess and the ensuing highly influential ‘scavenging debate’ (cf. Uthmeier 2006: 19), whilst ecologists increasingly stress the importance of apex predators in promoting biodiversity and species coexistence (Wallach et al. 2015).

Recent years have seen a resurgence of archaeological attention to carnivores, especially in the Late Pleistocene, due to a series of new discoveries revealing unusual hominin behaviors in relation to various carnivore taxa, both mammals and birds, including but not limited to the special treatment of whole skeletons or some selected body parts (e.g., Peresani et al. 2011; Morin and Laroulandie 2012; Walker et al. 2012; Romandini et al. 2014; Radović et al. 2015; Sanchis et al. 2015; Cueto et al. 2016; Sanz et al. 2017; Hussain 2019; Rodríguez-Hidalgo et al. 2019; Wojtal et al. 2020; Val et al. 2020; Hallett et al. 2021). This accumulating deep-time evidence clearly suggests that carnivores were more than mere evolutionary antagonists and may have contributed significantly, and in diverse contingent ways, to the human story over many millennia. Relatedly, Jimenez et al. (2021) have recently suggested to revisit the predatory sympatry of hominins and hyenas in Late Pleistocene Eurasia by rejoining palaeontology and archaeology and paying closer attention to how changing behaviors of key predators ‘orchestrated’ the behavior of their interlocutors – both prey and competitor – and in this way modulated broader co-evolutionary dynamics on ecosystem scales.

The present paper joins this broader call but proposes that a conceptual reframing of the study of Pleistocene hominin-carnivore relationships is required in order to fully explore the vital importance of nonhuman carnivores in the broader context of early human biocultural evolution. Carnivores need to come into view not only as evolutionary competitors, but equally so as co-constituents, perhaps even protagonists (Hussain *in press*) of the phenomenal and cognitive worlds in which past hominins operated, so that precarious hominin-carnivore communities and more-or-less stable neighborhoods can be investigated, detailed and contrasted from the perspective of integrated ecocultural analysis. This opening up of the conceptual space for examining hominin-carnivore intersections and their situated variability in deep prehistory provides new possibilities for integrating multispecies theory and the achievements of the widely celebrated ‘animal turn’ across the humanities and social sciences (Ritvo 2007; Haraway 2007; Kirksey and Helmreich 2010; Wolfe 2011; DeMello 2012; Ogden et al. 2013; Grusin

2015; Kalof 2017; Pilaar Birch 2018a). Combining these bodies of theory with more traditional palaeoecological and archaeological analysis and insight, whilst nurturing knowledge from general forager anthropology, discloses fresh perspectives on the interdigitation of hominin and animal lives in the Pleistocene past, and the centrality of changing hominin-carnivore interstices in the evolution of hominin lifeways and ecocultural adaptations.

The paper first outlines some basic multispecies concepts to facilitate the study of human-carnivore interactions, in particular its generative cultural and material dimensions. We then turn to the archaeology of Marine Isotope Stage (MIS) 5-3 Neanderthals in different parts of Europe as a case in point and explore their complex ecocultural entanglements with raptors, hyenas and bears. This exploration indicates that at least some instances of Neanderthal material culture previously interpreted as ‘symbolic’ can be framed as ‘emergent materialities’ of cohabitation and persistent friction between hominins and significant carnivore others in the landscape. We map these instances vis-à-vis *situated interspecies immediacies* following the seminal work of Bird-David (1990, 1994, 2017a). Finally, we examine the broader implications of this redressing of hominin-carnivore relationships, especially with regard to understandings of ‘nature’ in the deep past and problematic yet persisting narratives of accumulating hominin ‘modernity’ during the Late Pleistocene (cf., Nowell 2013; Ames et al. 2013; Porr and Matthews 2017; Kissel and Fuentes 2020). As an alternative reading ‘against the grain’, we suggest that much of the palaeoarchaeological evidence routinely mustered to bolster modernity narratives and related views in the field may in fact express diverse hominin-world engagements, i.e., the shifting roles of different nonhumans, including carnivore others, in various hominin affairs and the evolving modes and efforts of distributed multispecies ‘world-making’ (cf. e.g., Goodman 1978; Anderson and Harrison 2010; Descola 2010a, 2014; Stewart 2010). We propose there is a large, yet hitherto uncharted field of investigation where evolved carnivore legacies can fruitfully be exposed by investigating the co-evolutionary matrix of human-carnivore interaction and its consequences for and sociomaterial imports to multiple trajectories of becoming human.

## 2. Multispecies theory

At the core of multispecies thinking and cognate bodies of theorizing is a growing epistemological unease with the Western legacy of centering the human species in cultural and evolutionary processes (e.g., Kohn 2013; Nance 2015; Locke and Münster 2015; Boyd 2017; Armstrong-Oma 2018; Swanson et al. 2018). Critiqued are especially those variants of anthropocentric analysis in which radical domain autonomy is assumed and explicitly defended (Livingston and Puar 2011), to the extent that human affairs are portrayed and explained in complete isolation from the so-called phenomena of ‘nature’ (Anderson and Perrin 2018). Notwithstanding, multispecies theorists are equally adamant in their fundamental critique of undifferentiated, homogenizing and over-expansive views of nature and what is then symptomatically framed simply as the ‘external’ environment (Descola and Pálsson 1996; Descola 2005), more often than not falling back into naive ecological determinisms or perpetuating global or even universal heteronomy pre-suppositions. Yet humans, their behaviors, cultures and adaptations can hardly be analyzed or understood in separation from the diverse natures in which they partake (Hastrup 2014). To the contrary, human behaviors, material cultures and sociocultural horizons are always enfolded in, and to this effect partly a consequence of, variegated hybrid assemblages of humans and nonhumans and their situated internal dynamics, feedbacks, short and long-term histories, path dependencies and relational logics (Descola 2010b; Arluke and Sanders 2008).

Following Haraway (1991, 2016), the ‘multispecies condition’ of human life on Earth eclipses equalizing tendencies of ‘naturalization’ precisely because humans do not evolve in contradistinction but in connection and community with the heterogeneous repertoire of

nonhumans, including other animals, with whom they share their surroundings (cf. Lestel and Hollis 2013; Brittain and Overton 2013; Armstrong Oma and Goldhahn 2020). Due to this foundational anti-essentialist inclination, multispecies thinking promotes, and often joins forces with, relational approaches to human-nonhuman configurations in the past and their often far-reaching behavioral and socio-cultural consequences (Watts 2013a; Hill 2013; Harrison-Buck and Hendon 2018) – sometimes flagged as the ‘relational view’ in archaeology (Herva and Lahelma 2020; Wisner and Kay 2020). What Shipman (2010) has termed the ‘animal connection’ in human evolution is then much more than mere addendum to a list of evolved, supposedly quintessential human traits. Rather, as Tsing (2012) has poignantly noted, ‘being human[, then,] is an interspecies relationship’ (emphasis added).

In what follows, we delineate a number of key concepts derived from this expanding corpus of multispecies theory in archaeology, anthropology and relevant neighboring fields, especially from what is now routinely labeled ‘animal studies’, ‘anthrozoology’, ‘multispecies ethnography’ and, increasingly, ‘multispecies archaeology’. This exercise is necessary to prepare the stage for our subsequent attempt of redressing hominin-carnivore relationships in human deep prehistory.

### 2.1. Coevolution

The multispecies critique has important ramifications for how we think about human evolution and what place we secure for human-animal relationships in evolutionary dynamics. The agents of nonhuman nature, especially sentient animal others, draw attention not only as fuel, resources and raw materials of evolution or as fierce competitors, they come into view as potent and consequential *media* of evolution, altering the conditions and modes of evolutionary dynamics themselves (Hussain in press). Animals are not merely acted upon by humans or other towering, anonymous evolutionary forces (Naiman 1988), they can emerge as direction-giving protagonists within such processes (e.g., Jones et al. 1997). The often-underrated agency of animal others (pace Sultan 2015; Walsh 2015) comes for example to the fore when animals enter co-evolutionary relationships with hominins and play a role in fashioning local environments or creating behavioral opportunities and affordances for their hominin neighbors (e.g., Tchernov 1984; O’Connor 2013; Pierotti and Fogg 2017; Kost and Hussain 2019; Hjørungdal 2019). Hominins may then adapt to particular animal ecologies or specific animal species and the same may occur *vice versa*: nonhuman animals attend and adapt to particular environments, behaviors and behavioral possibilities catered by hominins (Haynes 2006; Clucas and Marzluff 2011; Boivin et al. 2016; Bocherens 2018). When both conditions are met, we can speak of *reciprocal* coevolution – or mutual ‘facilitation’ (Bruno et al. 2003) – which frequently produces intimate multispecies entanglements molding the long-time histories of those involved (cf., Fuentes and Wolfe 2002; Albarella et al. 2007; Sykes et al. 2020). Some of these strands of co-becoming can be framed as processes of ‘interspecies niche construction’ (Candea 2010; Fuentes 2010) in which humans and nonhumans modify and redress each other’s environments, and in this way alter the ecology-behavior nexus in larger, co-evolving multispecies communities (Pilaar Birch 2018b; Kost and Hussain 2019).

Importantly, such intimate co-evolutionary interlacings of hominins and other animals are premised to result in tangible and often unique cultural consequences, affecting for example how hominins move in their landscapes and organize their settlement systems, how environments are materially and cognitively appropriated, how material culture and hominin technology mediate encounters with various nonhuman others, and how hominins perceive, emplace, enstory and conceptualize the worlds they inhabit. Co-evolutionary linkages with animal others have thus the potential to reconfigure the totality of hominin behavior and cognition and this should be reflected in the various ways Pleistocene hominins have made themselves at home in specific animal landscapes and ecologies.

Haraway (2016: 58) reminds us that no living beings fully make themselves, and the same principle applies to human evolutionary processes – stipulated as ‘autopoietic’ or self-making, human evolution becomes a hollow, tractionless concept. Childe’s (1936) credo ‘man makes himself’ is thus at best misleading insofar as the human story hardly marks out a self-sufficient development, but rather bespeaks of complicated, distributed, multi-responsive, co-adaptive and situated trajectories, in which heterogeneous forces and agents, including hominins and other animals, engage with one another and probe into the emerging possibilities of co-existence and ‘being-with’. This constant tangling and cross-pollination of variegated evolutionary subjects that, in various ways and to varying extent, *make each other* is captured by Haraway’s (2007) now classic formulation of the ‘humanimal’ – the inescapable and historically significant co-making of hominins and animals, arguably exploration-prone especially in the thickets of deep time (sensu Shryock et al. 2011).

In this formulation, evolution is fundamentally a ‘sympoietic’ process (Haraway 2016) – change is predicated on ‘making-with’ – and *sympoiesis* becomes a key mechanism and driving force of hominin evolution writ large. Becoming or evolving is then almost always a process of ‘becoming-with’ (cf., Kirksey and Helmreich 2010: 546), so that the creation of ‘mutual ecologies’ (Fuentes 2010) and the articulation of hybrid ‘contact zones’ (sensu Pratt 1991, 2008: 8; cf., Aisher and Damodaran 2016; Isaacs and Otruba 2019) in hominin evolution become privileged loci of investigation, drawing attention to the delicate coordination of multiple lifeworlds and livelihoods that steer the directionalities of long-term change. Coevolution thus tables a range of useful concepts to incorporate more-than-human thinking into emerging contemporary approaches to human evolution – for example in the spirit of Fuentes’ (2015) call for an ‘integrative anthropology of the human niche’. In general, sympoiesis can be especially powerful, and may even become an overwriting process, when humans and other animals encounter each other as key ingredients and perceptual touchstones of their respective lifeworlds, and hence when animal others emerge as ‘companion species’ (sensu Haraway 2007). These salient animals are prone to co-configure the emotional, psychological and empathic horizons of their hominin interlocutors (cf., Hussain and Breyer 2017) and to foster particular emotive responses – e.g., respect, awe, curiosity or fear – that derive from the ethology of the animals in question and the nature of specific human-animal engagements, and in this way become paramount in shaping the experiential regimes and emotive topologies of the lifeworlds they share and co-make with hominins.

### 2.2. Interspecies immediacy and proximity

Over the last decades, animal studies and anthrozoology have begun to describe and map out variegated forms of interspecies relationship that arguably *are* human nature, and try to reframe archaeologists’ and anthropologists’ traditional concern with animals as ‘good to use’, ‘eat’ (Harris 1985) or ‘think with’ (Sax 2001) in favor of the historically situated conditions of shared multispecies life (Haraway 2007; Kirksey and Helmreich 2010: 552; Lestel and Hollis 2013; Brittain and Overton 2013; Locke 2014; Hussain 2019, in press). This emphasis on shifting constellations of *living together* opens up an entire set of animal-related research questions: e.g., how do hominins and animals overlap (or not) in geographic space? When and how do their behaviors intersect? What is the nature of their encounter and is the latter framed by particular places or mediated by specific materials and technologies? What are the cultural and biological rhythms that hominins and other animals attend to, and how are these related? What are the affordances provided by the respective other? How salient and regular are encounters and interactions between the involved agents? What cultural and material resources are activated and what strategies are deployed (if any) to ensure auspicious coordination, co-habitation and mutual respect? The relationship between ‘living-with’ and ‘becoming-with’ hereby recapitulates the intersection between ecology and evolution in

biology, but the accent is put on different ways of relating and engaging at shifting multispecies interfaces, in turn born out of the dynamics generated by historically-specific assemblages containing hominins, other animals and larger biophysical landscapes. Such multispecies interfaces are never entirely stable but mutable and open to reorganization (Livingston and Puar 2011). Their characterization thus requires careful analysis of how different life-processes and behaviors interconnect and resonate with one another, and what the specific ecological, socio-cultural and material consequences as well as creative potentialities are.

This life-oriented rendering of hominin-animal interaction draws attention to the *topologies of interspecies immediacy* (cf., Locke 2014; Hussain and Breyer 2017; Bird-David 2017a) and motivates their analysis and comparison. Hominins never lived in exclusionary enclaves of conspecifics, but had regular and often intimate contact with nonhuman others when operating in their environments (cf., Hussain 2019). There is a non-arbitrary relationship between the significance and nature of these contacts and the cultural and social technologies devised to respond to, curate, and process them. A brief ethnographic intervention is required to elaborate this point. As Bird-David (1994, 2017a, 2017b, 2018) and others (e.g., Meillassoux 1973; Price 1975) have lucidly unpacked in a number of writings, many small-scale foraging people – especially those attuned to a ‘band-like’ form of social organization – pursue their livelihoods in a general condition of immediacy. Despite the pronounced diversity of hunter-gatherer lifestyles, forms of social organization and intracommunity relations especially in the past (cf., Finlayson and Warren 2017), there is often little spatial and temporal segregation of the social world, i.e., hardly any boundaries of interaction and communication (Bird-David 1994: 591). Moreover, many small-scale societies tend to resist sociodemographic upscaling (cf. esp., Bird-David 2017b, 2018) and their ‘tiny-scale’ is not just a matter of numbers and effective population sizes or demography structures, yet is linked to the cultivation of culturally-specific scaling practices, or the premediated lack thereof (cf., Fowles 2018), which in turn feed into regulative ideas of world-making and sociality, fundamentally regulating how these foragers perceive and attend to their world (Bird-David 2017b). The small size of these communities, often bound to an ethos of ‘total sharing’, has particular consequences for their modes of being-with conspecifics but also with nonhuman others with whom the local environment is co-inhabited and shared. Small-scale societies, especially those adhering to ‘immediate return’ modes of production (Woodburn 1980, 1982), thus tend to inhabit intricate ‘nanoscale’ worlds (Bird-David 2017a) where social and ecological distance is considerably reduced and ‘immediacy’ often actively sought-for, created and behaviorally facilitated. Forager life in these socioeconomic contexts is characterized by an intrinsic quality of *co-presence* (pace Widlok 2020) – or by what Bird-David (2017a, 2019) has called ‘pluripresence’ – and this quality readily extends beyond the limits of the human, also encompassing multispecies relationships and understandings.

Conditions of pluripresence, which are commonly tied to close-knit and non-exclusionary communities of practice, interaction and routine encounter, often with deep knowledge of local ecologies and heightened levels of social transparency, easily give way to *expansive* ‘we understandings’ and ‘designations’ (Bird-David 2017b). These can accommodate a significant number of nonhuman members, especially if they constitute phenomenological cornerstones and key agencies of the immediate environments in question – i.e., animal others who are frequently witnessed, recurrently encountered and those who typify or markedly shape these local surroundings. The commonality, and in some cases near-banality, of their being-with humans creates a sense of sharing, belonging and tangible companionship that goes hand in hand with sociocultural adjacency and proximity. As Bird-David (2017a, 2017b) points out, the central trope and experience in these contexts is *phenomenological diversity* and not homogenization, and such basal diversity crosscuts the Western human-animal boundary. The key point is that nonhuman others are capable of entering the wider social field of these forager societies (Hussain 2013; Langley 2013; Hussain and Breyer

2017: 216-218) and ‘society’ can become a near-synonym for the social bonds that permeate human-nature systems as a whole (Descola 1996, 2005; Bird-David 1999; 2017a; Bird-David and Naveh 2008; cf., Bawaka Country et al. 2015). Just like other members of society, socially recognized nonhumans co-configure the specific ‘horizons of concern’ (Bird-David 2017b) that anchor the everyday activities and occupations of their forager neighbors.

Life in phenomenologically ‘small worlds’ therefore lays the foundations for real and ‘imagined’ multispecies communities (pace Anderson 1983) and can afford more-than-human belonging and kinship (pace Haraway 2016), even if the modes of ‘being many’ might differ across time and space. Under conditions of pluripresence, there is reduced social pressure to *address* the already-present, yet multispecies neighborhoods are nonetheless culturally cherished and often require material and cultural negotiation and coordination, especially if lived or experienced as precarious. These consequential more-than-human configurations can for example be examined by confronting human and nonhuman geographies (Bennett 1960; Wolch and Emel 1998; Ogden et al. 2013; Baynes-Rock 2013; Rutherford and Wilcox 2018), affective multispecies landscapes and places (Ogden 2011; Overton and Hamilakis 2013; Lorimer et al. 2019) and the distribution of more and less mobile elements such as artefacts in them, including their fragmentation, circulation and deposition. Some tiny-scale forager societies also seem to engage in behaviors that register as ‘distance-reduction’ strategies, and hence increase proximity between humans and nonhumans, sometimes even extending to the inanimate, for instance when stones and other ‘natural’ objects are brought to occupational spaces in order to ‘live with’ and accompany people (Bird-David and Naveh 2008; Bird-David 2018: 312).

Indigenous thinking similarly highlights the pluralistic nature of society-making based on the ‘circulation of agency through human and nonhuman worlds’ (Watts 2013b) as well as the maintenance and careful curation of foundational social relationships with other-than-human entities such as animals (TallBear 2011; Todd 2014; Musharbash 2017; Maynard 2022). What counts as ‘society’ not only depends on human practice and thought then, but also critically relies on how both are enfolded in larger multispecies landscapes populated by stones, rivers, plants and other-than-human animals (Watts 2013b). This agential ‘heterotopology’ of space is anchored in lived experience of co-being and interspecies proximity and directly bespeaks of the mutable architecture of situated multispecies lifeworlds, hence emerging as a precondition rather than a consequence of significations of ‘place’ and how the land (‘Country’ in many Indigenous conceptions, cf. Bawaka Country et al. 2015) is navigated, storied and enculturated (Todd 2017). Recognizing society as a species-transcending process of multi-agential polyphonic participation, in which human-animal boundaries are encated as fluid and continuously re-negotiated, rather than cast as categorically invariant, is part of broader decolonization efforts in anthropology and archaeology and as such tables new resources to develop and probe into alternative ways of exploring and understanding the Pleistocene past (Steeves 2021).

Indigenous thinking further draws attention to the structural connection between human-nonhuman co-becoming, interspecies coordination and the importance of cultivating attentiveness and cultures of respect, care and responsibility in the face of nonhuman others (Bawaka Country et al. 2015). Indigenous perspectives highlight the centrality of ‘more-than-human geographies of care’ that begin rather than end with a ‘social ontology of connection, foregrounding social relationships of mutuality and trust’ (Lawson 2007: 3). This is not to say that these relationships are always bound to be harmonious or positively sanctioned, to the contrary, it emphasizes their porosity and the resulting need to continuously labor them and their success for the sake of physical, social, emotional and cosmological sustenance. Connection, respect and co-responsibility are not abstract theoretical notions, then, but are retrieved from lived experience and situated, embodied interactions in the concrete context of a lifeworld stained in

proximity, where humans and nonhumans inexorably ‘share[] time, space, resources, and experiences of *both good times and the bad*’ (Musharbash 2017: 109, emphasis added).

### 2.3. Naturecultures

Multispecies considerations collapse the fundamental distinction between nature and society, and thus undermine the tenets of dualist theory (Haraway 2007, 2016; Kirksey and Helmreich 2010; Baynes-Rock 2013, 2015a). Multispecies being-with and becoming-with cannot properly be elucidated when adhering to an analytical separation between ecological and sociological orders, such that the ‘former is primarily an extension of the order found everywhere in nature, whereas the latter is exclusively, or at least almost, a distinctly human phenomenon’, often with an explicit coupling of ecology and competition vs. social organization and communication (Hollingshead 1940: 358). This classic Western dualist view of human-nature relations – inscribing either into ‘orientalist’ or ‘paternalist’ paradigms (sensu Pálsson et al. 1996) – can be contrasted with a paradigm of ‘communalism’ emphasizing that notions of ‘nature’ and ‘society’ are at best products of or nodal points within a continuous, dialogical process of co-making among heterogeneous actors (Pálsson 1996: 72; cf. Descola 1994, 1996). This focus on *dialogue* not only enables to take into account that hunting-gathering people and animal others are known to engage in the ‘mutual production of each other[’s realities]’ (Tapper 1988: 52), resisting the ‘Othering’ of nature so central to the Modernist project (Pálsson 1996: 64), but also, and perhaps more importantly, to recognize the possible alterity and non-analogicity of human-nature constellations in comparative deep-time perspective, while remaining inclusive and sensitive to Indigenous knowing.

The rejection of orientalism and paternalism and their problematic discontinuous framing of the human-nature nexus in favor of communalism centered on human-nature continuity as well as contingent, situated and participatory forms of generalized, although often non-balanced reciprocity (cf., Pálsson 1996: 66–67, 72) provides a productive vision of variously textured ‘naturecultures’ (sensu Haraway 2003: 1–5; cf., Potter and Hawkins 2009; Malone and Ovenden 2017) available for interdisciplinary investigation and confrontation. The material residues, artefacts and signatures recovered by archaeologists are then, on a basic level, to be considered first and foremost ‘emergent materialities’ of such shifting nature-culture interlacings, rather than ‘expressing’ or ‘representing’ mysteriously pre-assembled natural or cultural capacities; they are both the means and outcomes of changing articulations of humans and nonhumans and their mutable modes of attending, co-making and sympatry. Distinct naturecultures and their specific socio-material productions and generative relations are likely bound up with different ‘styles of worlding’ (Descola 2014), and as such help to illuminate, or at least draw near, the ontological contours of past hominin lifeways in unique multispecies worlds.

### 3. The sympatric Neanderthal

In an early review of human-animal interactions in hominin pre-history, Mithen (1999: 198) concluded that ‘Neanderthals did not develop any relationships with animals beyond those of predator/prey as had characterized human ancestors for the previous million years’, and that ‘the role animals played in Neanderthal society was [therefore] limited’. More recently, Shipman (2010, 2015a) has suggested that the establishment of consequential and permanent social ties with animal others, primarily through early forms of domestication or self/autodomestication, remains a milestone achievement of *Homo sapiens* populations, and thus possibly contributed to the competitive disadvantage of Neanderthals and other Late Pleistocene hominins in Europe and elsewhere (esp. Shipman 2015b). Mithen (1996, 2013: 221) has further weaved his view into a ‘cathedral model’ of the mind, explicitly denying Neanderthals any domain fluidity and thereby reinforcing problematic

modernist nature-culture polarities. In a similar spirit, Langley (2013), albeit not explicitly discussing Middle Paleolithic human-animal interfaces, has suggested that Neanderthals had a limited capacity to ‘socialize’ their landscapes, and developed material culture such as personal ornaments primarily to mediate interpersonal relationships rather than to negotiate hominin-animal-place linkages. Symptomatically, animal historians also tend to start their exploration of animal contributions to human history with opulent *H. sapiens* cave art and the manipulation, management and domestication of nonhuman animals at the Pleistocene-Holocene threshold (e.g., Kalof 2007).

We suggest that this received view reflects a fundamental misunderstanding of Neanderthal society promoted by a narrow discourse on hominin modernity and so-called symbolic capacities plaguing the archaeological expert literature for many years now. Neanderthals and other Late Pleistocene hominins were deeply attuned to their local animal ecologies and developed varied forms of interspecies sympatry with so far overlooked consequences for hominin life and materiality. Rethinking Neanderthal-nature relations in the light of multispecies theory requires to take seriously that animal ecologies and interspecies relations may have been basic cultural resources for these hominins. This necessitates moving past binary disciplinary discourses, which continuously re-cast Neanderthals in terms of a ‘us’ vs. ‘them’ logic (Speth 2004), either overemphasizing difference or similarity (cf. e.g., Villa and Roebroeks 2014). This conceptual deadlock and the resulting imaginaries of Neanderthal behavior have trickled down to and fundamentally biased the study of Middle Paleolithic hominin-animal interactions, which continue to be examined almost exclusively in ecological and economic terms (Priestley 2020). What is more, recovering the purportedly ‘symbolic’ dimensions of Neanderthal behavior (e.g., Finlayson 2019) may only worsen the situation since symbolism is rarely unpacked and placed in its deep-historical context, but more often than not serves as a privileged lighthouse of affirming hominin ‘capacities’ and cognitive dispositions. A phenomenological approach helps to lay bare and explore the specificity and historicity of Neanderthal engagements with the nonhuman world without retreating to normative juxtapositions of Middle and Upper Paleolithic hominins.

Phenomenology also matters when the social dimension and immediacy of Neanderthal being-in-the-world is taken into account. Neanderthal societies were tiny-scale – as indicated by the scattered nature of their material traces (e.g., Jöris 2014: 1724–1726; Loch et al. 2016), the size and palimpsest character of their sites, living spaces, shelters and settlement structures (Kolen 1999; Uthmeier 2006: 25; Hayden 2012) as well as the latest palaeodemographic reconstructions and interpretations (Stiner and Kuhn 2006; Bocquet-Appel and Degioanni 2013; Mafessoni and Prüfer 2017; French 2021). Their socioeconomic strategies, furthermore, presently lack substantial evidence for the storage and delayed consumption of food, labor-intensive trapping and catching devices or supports such as nets and boats, the organized manipulation of wild plants and/or animals, and differential access to some of these resources within their communities (pace Woodburn 1982: 432–433). Taken as a whole, this signals their broad operative reliance on ‘immediate return’ foraging systems (in contrast to ‘delayed return’ systems; sensu Woodburn 1980), albeit likely without direct historical or contemporary analogues, and despite increasing evidence for general niche construction capacities (Roebroeks et al. 2021; Nikulina et al. 2022). Strikingly, recent eco-cultural niche modeling of Middle Paleolithic Western Europe, in particular France, suggests that Neanderthal groups displayed pronounced territorial integrity and region-fidelity (Banks et al. 2021), which, together with their high mobility profile (Jöris 2014), would have amplified their ecological intimacy and exposure to particular animal-ripe ‘giving environments’ (pace Bird-David 1990; see above).

The archaeological record of Neanderthals in Europe includes evidence for practices of social care (Spikins et al. 2018) and plant-based medical knowledge (Hardy et al. 2012) – and thus potential ‘social technologies’ of delayed return – but there is no unambiguous

subsistence-related evidence satisfying the original definition of delayed-return foragers (sensu Woodburn 1982; cf., Uthmeier 2006: 24). That said, some researchers have argued that the apparent spoil surplus implied by some Neanderthal kill and processing sites may indicate meat storage and tactics of ‘deferred’ consumption with low archaeological visibility (Rendu et al. 2012; Speth 2017; Wragg Sykes 2020: 165). Further, Neanderthal stone working and tool-use technology is certainly more complex and presuppositional than often acknowledged (Çep et al. 2021). Middle Paleolithic lithic technology is frequently anchored in coexisting *débitage* and *façonnage* systems including more-or-less specialized operational sequences and tool concepts showcasing considerable technical planning-depth as well as operative delayed-return rationales (e.g., Soriano 2000; Soressi and Hays 2003; Delagnes and Rendu 2011; Turq et al. 2013; Weiss 2020). Yet overall, economic intensification remains to be convincingly demonstrated at least for European Neanderthals (see Speth and Clark 2006 for possible Levantine evidence) and the small number of pit and ‘scoop’ features known from Middle Paleolithic contexts, for example at the classic site of La Quina in Western France, have mostly been interpreted as non-alimentary structures (cf., Debénath and Jelinek, 1998: 37; Pettitt 2002: 18; but see Speth 2017: 62).

Furthermore, the Western Eurasian Neanderthal record and its human-animal relations are not as homogeneous as they have long been pictured (Mithen 2006: 230-231; de la Torre et al. 2013; Kuhn 2013; Angheliu 2014). There is now increasing evidence for varied material and subsistence practices and sociomaterial entanglements with various animals and ecological assemblages in different spatiotemporal contexts (Stringer et al. 2008; Nowell 2013; Churchill 2014: 185; Roebroeks and Soressi 2016; Shipley and Kindscher 2016; Morin et al. 2016; Villa et al. 2020), pointing to a heterogeneous and bafflingly complex chrono-geography of Neanderthal naturecultures and ecocultural regimes (cf., Wragg Sykes 2020 for a similar global argument). This diversity has previously been explained by the ecological flexibility of Neanderthal populations and their ability to successfully adapt to local conditions (Churchill 2014), but a closer look at the intersection of local multi-species assemblages, animal agencies, Neanderthal behaviors and material productions reveals the limitations and lack of context-specificity of such explanations, glossing over the phenomenological ramifications and challenges of Neanderthal life in disparate multispecies arenas (cf., Wragg Sykes 2020: 221-225). Similar concerns have led Chang and Nowell (2020) to advocate an ‘ethnographic’ approach (in opposition to ‘ethological’) to the Neanderthal record in order to account for the diverse ecological, social and cultural lives of these Late Pleistocene hominins, and, one should add, their hominin-animal intersections. Their call resonates with Lestel’s (2006: 150) efforts to pave the ground for a vigorous synthesis of ethology and ethnography in the behavioral sciences more broadly, arguing that the ‘evolution of social complexity needs to be rethought’ in light of hybrid human-animal societies ‘sharing meaning, interests and affects’ and which are ‘more often the norm rather than the exception.’

Given that ‘nature’ and ‘culture’ are distinct categories of Western modernity and often have only limited value for understanding small-scale foraging societies (Viveiros de Castro 1996; Pálsson 1996; Bird-David 1999; Descola 2005, 2010b, Kohn 2013), the search for explanations should also not prematurely stop at the fringes of subsistence strategies, Neanderthal resource management and behavioral ecology. Instead, Neanderthal scholarship must actively explore the multifaceted significance of varied hominin engagements with the non-human world, including non-animate materials such as stone, ivory and bone (cf. esp., Conneller 2011) as well as living organisms such as plants and animals. Current dualist theory – the default point of departure for most Pleistocene archaeologists – too often suggests, or simply takes for granted, that hominin behaviors and material signatures not directly tied to the fulfilment of the basic requirements of survival and ecological adaptation are the only residuals of culture, and as such earmark milestone cognitive and sociopsychological achievements in hominin evolution (e.

g., Renfrew and Morley 2009; Henshilwood and d’Errico 2011; Hofecker 2017). Those behaviors supposedly intelligible by the lower rungs of the Hawkesian ladder of inference (pace Hawkes 1954) are in turn considered to be confined to ‘lower’ domains, with no obvious or knowable implications for ‘higher’ domains such as culture and cosmology. This has reinforced the tendency in Middle Paleolithic research to cut off the discussion of hominin culture from hominin subsistence, even though hunting is a key locus of culture and sociality in hunter-gatherer societies (cf., Ingold 2000; Nadasdy 2007; Bawaka Country et al. 2015, see discussion below), and thus to refrain from more-than-economic, integrative and holistic approaches to Neanderthal-animal interaction.

The classic example for this broader logic of research enveloping other-than-*H. sapiens* prehistory is the handling of archaeological evidence for the dislocation of so-called ‘unusual’ or ‘exotic’ objects, mostly unaltered but sometimes materially manipulated and incised (cf., Marshack 1991: 47-48; Peresani et al. 2013, 2014; Leder et al. 2021), such as fossils, shells, minerals and prominently colored or textured stones, and their incorporation into hominin sites (Bolus and Schmitz 2006: 139; Radović et al. 2015; Wilkins et al. 2021). The received dualist narrative identifies these alleged ‘curiosities’ as signposts of a dawning ‘sense of aesthetics’ and, relatedly, as emerging ‘proto-symbolic capacities’ in the hominin lineage (Bednarik 1994; Mellars 1996: 371; Lorblanchet 1999; Frayer et al. 2020). Lorblanchet and Bahn (2017: 55) for example confidently assert that ‘the first humans had a sense of aesthetics, and [...] they were even endowed with a certain delicacy of touch. Their behaviour seems very close to our own, as we continue to pick up shells, fossils and other natural curiosities’. The manifold examples mobilized in support of this narrative occupy a salient place especially in Neanderthal archaeology (e.g., Frayer 2019), where they are recurrently evoked to bolster the popular idea that these hominins were in many ways ‘like us’, thereby exposing problematic *H. sapiens* benchmark assumptions which at times even develop into different forms of sapienscentrism and thus once again revealing the blatant universalist lens that is too frequently deployed in this debate. In point of fact, it is often unclear what exactly eruditions of the above-cited type are supposed to disclose: given broad comparative evidence for multi-sensuous experience, emotion, affect and even ‘aesthetics’ in many nonhuman animals (Bekoff 2002; Menninghaus 2011; Watanabe 2012), it seems neither surprising that affective factors played a role in shaping Neanderthal lifeways, nor is it entirely clear how the alleged archaeological recovery of such generalized qualities can assist in understanding the specificity of Neanderthal being and becoming beyond a broad trait-register logic.

From a multispecies and communalist perspective, psychological and proto-symbolic ascriptions detract attention from concrete lifeworld situations and sociodemographic contexts in which these objects make their archaeological appearance. Given that many small-scale forager societies consistently gather stones and other natural objects and for example also bring back seemingly abandoned animal puppies from their local surroundings in order to ‘raise them’ and/or ‘live with them’ (cf., Serpell 1989; Bird-David 2017b; Bird-David and Naveh 2008; Simonova 2018; cf., Shipman 2010 on ‘cross-species alloparenting’) at least indicates that deep-historical ‘curiosities’ and ‘manuports’ may similarly inform us about *practiced socioecological relations*, rather than being mere expressions of so-called ‘modern’ human behavior and cognition. Often-cited ‘non-utilitarian’ objects might thus derive from hominin-environment relationships characterized by acute and pervasive immediacy, rather than being the externalizations of hominin ‘essences’ and inborn qualities, and are then foremost to be regarded as varied forms of *material engagement* with the inhabited and continuously re-made more-than-human world. In this way, these objects can be acknowledged as potent pointers to situated hominin-ecology intersections and may revealsignifications and perpetual negotiations of extended small-world societies under conditions of pluripresence (pace Bird-David 2017a).

Instead of invoking the detached contemplative capacities and invariant aesthetic sensibilities of Neanderthals and other contemporary non-*H. sapiens* hominins, such 'special' objects may give testimony to shared and entangled multispecies life in which nature is not merely appropriated but integrated to, and as such part and parcel of, diverse efforts of past society-assembly, place-making and world-building. The respective objects, in this view, are drawn into hominin places and incorporated into occupational deposits not primarily because of their evocative materiality, but as a means of promoting relatedness and 'being-as-many' in more-than-human landscapes (Bird-David 2017a), and thus to affirm social immediacy. This yields an argument from 'horizontal' according to which human beings do not 'walk [...] on top of an ontological floor, but attending to and being attended by the bodies surrounding [them], some [] animated and some not, some solid and some liquid and gaseous' (de Carvalho Cabral 2021). Approached from this perspective, Middle Paleolithic curiosities provide evidence for distributed, nonhuman-focused 'horizons of concern' and related Neanderthal efforts to facilitate forms of mutual habitation that are both the 'continent and the content of life' (de Carvalho Cabral 2021) in a multispecies world. The concept of aesthetics that can be derived here

closely resembles what pragmatists have rendered as 'aesthetics of the everyday' (Sartwell 2009) or 'social aesthetics' (Coleman et al. 2013) – understandings that insist on the embedded nature as well as the interaction, experience and lifeworld-dependency of aesthetic certification (cf., Skeates 2017), hence undermining the dominant cognitivist interpretations in archaeology that emphasize inert pre-social and/or pre-lifeworld capacities with traceable biological, lineage-specific origins. As Welsch (2004) puts it, aesthetics, instead, emerges from mingled human-nonhuman layers of existence and is thus a derived property of more-than-human worlds and their sensuous conditions.

In what follows in the subsequent sections, we extend this perspective into the domain of nonhuman carnivores and explore the sympatric ecology of European Neanderthals with regard to raptor, hyena, and ursid others sharing the landscape with these hominins. By synthesizing the available evidence on Neanderthal engagement with these animals and putting the available data into multispecies and integrative anthropological perspective, we hope to show that valuable insights can be gleaned on Middle Palaeolithic lifestyles, adaptations and distinct naturecultures within and between different deep-historical contexts, and that sharing the landscape with other animals and attending to them

**Table 1**

Overview of manipulated raptor talons from the Middle Paleolithic and incipient Upper Paleolithic of Western Eurasia. Behavioral and ecological information on raptor species compiled from [birdsoftheworld.org/](http://birdsoftheworld.org/). \* Note that the Neuronian from Mandrin E has recently been reattributed to *H. sapiens*.

Site	Layer	Country	Marine Isotope Stage	Period	Species	Behaviour/Ecology	References
Combe Grenal	XV	France	MIS 3	MP	Golden eagle	Apex predator; occasional diurnal scavenger of larger animal carcasses; Golden eagles are sometimes killed by wolves, wolverines or larger cats while preying on ground carcasses; ravens are kleptoparasits of nesting Golden eagles	Morin and Laroulandie 2012
Fumane	A12	Italy	MIS 3	MP	Golden eagle		Romandini et al. 2014
Grotte de L'Hyene	n/a	France	MIS 3	MP	Golden eagle		Morin and Laroulandie 2012
Rio Secco	7	Italy	MIS 3	MP	Golden eagle		Romandini et al. 2014
Mandrin	E	France	MIS 4/3	MP (Neronian)*	Golden eagle		Romandini et al. 2014
Pech de l'Azé I	4	France	MIS 3	MP (MTA)	Golden eagle		Soressi et al. 2008
Grotte du Renne	IX-X	France	MIS 3	Chatelperronian	White-tailed eagle	Apex predator; highly opportunistic yet seasonally varied diurnal predatory behavior; White-tailed eagles are known for their perch-hunting style and in winter often live largely as scavengers, following or watching for other similarly feeding birds such as corvids, vultures and other smaller birds of prey	Laroulandie et al. 2020
Les Fieux	Rec. clean	France	MIS 3	MP (MTA)	White-tailed eagle		Laroulandie et al. 2016; Morin and Laroulandie 2012
Krapina	n/a	Croatia	MIS 5	MP	White-tailed eagle		Radović et al. 2015
Les Fieux	I/J	France	MIS 4/3	MP	White-tailed eagle		Laroulandie et al. 2016; Morin and Laroulandie 2012
Les Fieux	Jbase	France	MIS 4/3	MP (MTA)	White-tailed eagle		Laroulandie et al. 2016; Morin and Laroulandie 2012
Les Fieux	Ks	France	MIS 3	MP (MTA)	White-tailed eagle		Laroulandie et al. 2016; Morin and Laroulandie 2012
Les Fieux	Ks	France	MIS 3	MP (MTA)	Cinereous vulture	Solitary bird aggregating at large carcasses or other 'natural' feeding sites; specialized carrion-feeder of all carcass types; powerful bill to tear open thick carcass skin; often dominant over other vultures and scavengers in its range; known to adapt well and flexibly to human carrion landscapes (including human burial grounds and similar places)	Laroulandie et al. 2016; Morin and Laroulandie 2012
Grotte du Renne	IX-X	France	MIS 3	Chatelperronian	European eagle owl	Largely nocturnal predator; tends to be highly sedentary an maintains a well-defined territory/hunting ground throughout most of its adult life; extreme longevity; daily flight is usually caused by human interference or mobbing crows. In Iberia, Eagle owls have evolved within a predatory guild, alongside large eagles, largely feeding on rabbit	Laroulandie et al. 2020
Pech de l'Azé IV	8	France	MIS 5	MP	Unknown medium-sized raptor	n/a	Dibble et al. 2009
Cova Foradada	IV1	Spain	MIS 3	Chatelperronian	Imperial eagle	Apex predator; occasionally pirates food items from other birds of prey or predators; generally highly opportunistic diurnal predator; pair-hunting, especially during winter, is not uncommon; often feeds on corvids	Rodríguez-Hidalgo et al. 2019

in a regular manner often had decisive, long-lasting consequences for hominin behavior, society and material culture which archaeologists should begin to examine more systematically, in particular outside of the traditional confines of *H. sapiens* prehistory.

### 3.1. Raptors: Familiars who soar high

We suggest that understanding Neanderthal sensitivities towards, and engagement with, raptor others can benefit from paying more attention to the co-constructed naturecultures of Late Pleistocene hominins, vultures and other large birds of prey, instead of foregrounding, and thereby prematurely narrowing, the debate in terms of the alleged ‘symbolic’ proficiency of raptor-derived items of material culture (Finlayson 2019). From a multispecies and dedicated communalist point of view, the recurrent interest of Neanderthals in the talons, and perhaps wings and feathers (Romandini et al. 2016), of different large raptor species, especially Golden and White-tailed eagles (Negro 2018; Rodríguez-Hidalgo et al. 2019; Laroulandie et al. 2020), points to the significant intersection and emergent socioecological proximity between these hominins and raptor others. Given the predatory profile of Neanderthals at the top of the trophic pyramid of their ecosystems (Gaudzinski-Windheuser and Kindler 2012; Jöris 2014; Smith 2015; Wragg Sykes 2020) and the known structural impact of such social carnivores on their ecologies (Wallach et al. 2015), obligatory and facultative scavengers such as vultures and some large eagles, including the focal species documented in the Neanderthal record (Table 1), would have been drawn to these carcass-accumulating predatory hominins in order to take advantage of hominin-mediated feeding affordances (cf., Moléon et al. 2014). These opportunities can be direct or indirect (e.g., flushing of smaller and medium-sized animals when encircling larger prey, etc.), and are closely linked to the scheduling and nature of hominin behavior in the wider landscape (see Sick 1997 for a nonhuman example; cf., Galetti et al. 2018). Anthropogenic facilitation and opening up of attractive feeding niches for raptors, even though heterogeneous and varying in productivity and impact, is well-demonstrated in present-day contexts (e.g., Bird et al. 1996; Lambertucci et al. 2009) and there is no reason to assume that Pleistocene raptors would refrain from adapting to anthropic landscapes of opportunity.

White et al. (2016) have shown that Neanderthals, especially in interglacial environments, were often selective in their ungulate carcass processing behavior, and when taking advantage of favorable ambush-alleviating settings, frequently exploited only a subset of the killed animals in a comprehensive manner – especially at largely monospecific killsites documenting short-term mass death scenarios of animal prey such as the MIS 5/4 or MIS 4/3 site of Salzgitter-Lebenstedt (Gaudzinski and Roebroeks 2003; Gaudzinski-Windheuser 2006, 2021; cf. Pastoors 2001). Neanderthal subsistence behavior, in other words, would have created a carrion surplus in the wider landscape, which likely acted as a significant hominin ecosystem service mediating broader Middle Paleolithic carrion ecologies (pace Barton et al. 2013). Moreover, body-part transport patterns and inferred decision-making rationales have certified Neanderthals as ‘optimal foragers’ focusing primarily on the meat-heavy and nutritionally valuable portions of dead animals as well as importing and/or exporting mainly the respective gourmet parts (Costamagno et al. 2006; Gaudzinski-Windheuser and Kindler 2012; Rendu et al. 2012; Castel et al. 2017; Daujeard et al. 2019). While this behavior can justifiably be described as ‘optimal’ from an energetic perspective, it similarly implies that carcasses would often have been exploited only partially and in a targeted fashion, providing recurrent scavenging opportunities for other animal co-inhabitants in the same landscape (cf., Moléon et al. 2014: 397). As apex predators in their environments, Neanderthals, through their situated hunting behaviors, would have thus actively contributed to the construction of potent co-adaptive interfaces with other carnivores including vultures and occasionally scavenging eagles, hence amplifying the lifeworld association and intersection of hominins and raptors during the Middle Paleolithic.

‘Wasteful’ hunting has been discussed both for interglacial and glacial Neanderthals (Wragg Sykes 2020: 222, 230) and is evident at the high-resolution forested Eemian lakeshore environment of Neumark-Nord in Eastern Germany, where the close-quarter ambush of two prime-aged stags is linked to low intensity butchering and even the most heavily processed deer carcasses were filleted but not jointed (Gaudzinski-Windheuser et al. 2018; cf., Wragg Sykes 2020: 220-221). ‘Wasteful’ butchering has similarly been suggested for elephant carcass exploitation at Eemian Lehringen and Gröbern (cf., Thieme and Veil 1985; Mania et al. 1990). As Priestley (2020) has rightly pointed out, however, not only is it problematic to impose a Western conception of ‘waste’ onto otherwise highly strategic and ecologically perceptive Neanderthals (Uthmeier 2006), non-comprehensive carcass exploitation is actually fairly common among ethnographically-documented northern and circumpolar foragers. For the Yukaghir of Northeastern Siberia, for example, leaving parts of hunted animals at the killsite and being selective about what is taken back to human camp sites is a significant social and cosmological practice (Willerslev 2007: 34-35; Cleghorn 2017; Priestley 2020: 144-145). In a liminal world where bodies are never stable and contained, hunting easily becomes a ‘generative’ enterprise safeguarding the cycle of life and the sustenance of life processes (Jordan 2003) by submitting part of what has been taken to the land, and therefore literally sharing carcasses with other organisms.

For Neanderthals, hunting of large, meat-heavy ungulates and making ‘gourmet’ cuts as well as taking only highly praised pieces such as the tongue may thus have played a more-than-economic role by reproducing and reinforcing the intersection with prime animal scavengers, and in this way negotiating the hominin place as predators and hunters in a more-than-human world. The striking selectivity of Neanderthal bone utilization, perceptively noted by Wragg Sykes (2020: 149, 229), which seems to indicate particular cultural norms and meaningful, non-arbitrary associations between particular animal species, specific bones and tool manufacturing decisions and biographies (e.g., Martisius et al. 2020) is consistent with this interpretation and further illustrates the part-focused logic of Neanderthal prey processing and animal body transformation. As argued by Zahara and Hird (2015), drawing on Indigenous Inuit communities’ practices in the Eastern Canadian arctic, food leftovers and anthropogenic dumps are ‘waste’ only from a Western, phenomenologically-detached point of view and in other contexts often promote proximity between humans and nonhumans and hence facilitate the creation and perpetuation of shared multispecies communities and livelihoods.

It is notable that the guild of large avian scavengers was also much larger in the Late Pleistocene than it is today, encompassing vulture species of considerably larger body-size and biomass recycling capacity than their surviving Holocene sister taxa (Hertel 1994; Galetti et al. 2018). Neanderthals and avian scavengers thus participated in broader ecological dynamics rendering the Plio-Pleistocene epochs particularly diverse in scavenging species and niches, both terrestrial and airborne, and in the latter case also comprising other birds such as the highly flexible *Corvidae* (Galetti et al. 2018). On palaeoecological grounds alone, many of these species were most likely co-adapted and were thus dependent on their respective trophic interaction(s), including emerging forms of sympatry and commensalism, as recently already proposed by Gómez-Olivencia et al. (2018) for eagles and Iberian Neanderthals. The close association between Pleistocene megafauna, involving Neanderthals and other hominins, and facultative or expert avian scavengers (Finlayson et al. 2012), must therefore be regarded not only as evidence for their landscape sharing and heightened ecological overlap, but similarly as a testimony of interspecies co-becoming, promotion and reliance.

The co-occurrence of Neanderthal, raptor and corvid signatures across large parts of Pleistocene Eurasia (Finlayson and Finlayson 2016) would then appear to primarily denote a multispecies assemblage rooted in significant, lived interspecies ties, encounters and consistent associations rather than indexing ‘advanced cognitive capacities’ or the

'ritual', 'symbolic' or 'religious' status of the birds in question (sensu Finlayson et al. 2019). As Wragg Sykes (2020: 259) has noted, eagles and 'early adopter' commensals such as crows and ravens (pace O'Connor 2013) participated with particular roles in the intra-scavenging guild dynamics of their time (Moléon et al. 2014) and were probably 'familiar' at Neanderthal killsites, even though birds such as choughs were likely encountered not only in the open landscape but also in their cave roost sites (Blanco et al. 2021). There is therefore certainly a striking congruence between the archaeological co-occurrence of Neanderthals, raptors and eagles and their attendance in a shared ecological microcosm of post-kill relationships and biosemiotics ties. Eagles have for example been shown to often rely on clues from corvids to detect carcasses (Grubb et al. 2018; Orr et al. 2019) and eagles, in turn, alert and thus 'call-in' vultures (Kane et al. 2014), giving rise to distinct post-kill biographies of Neanderthal killsites fundamentally centered on these avian others.

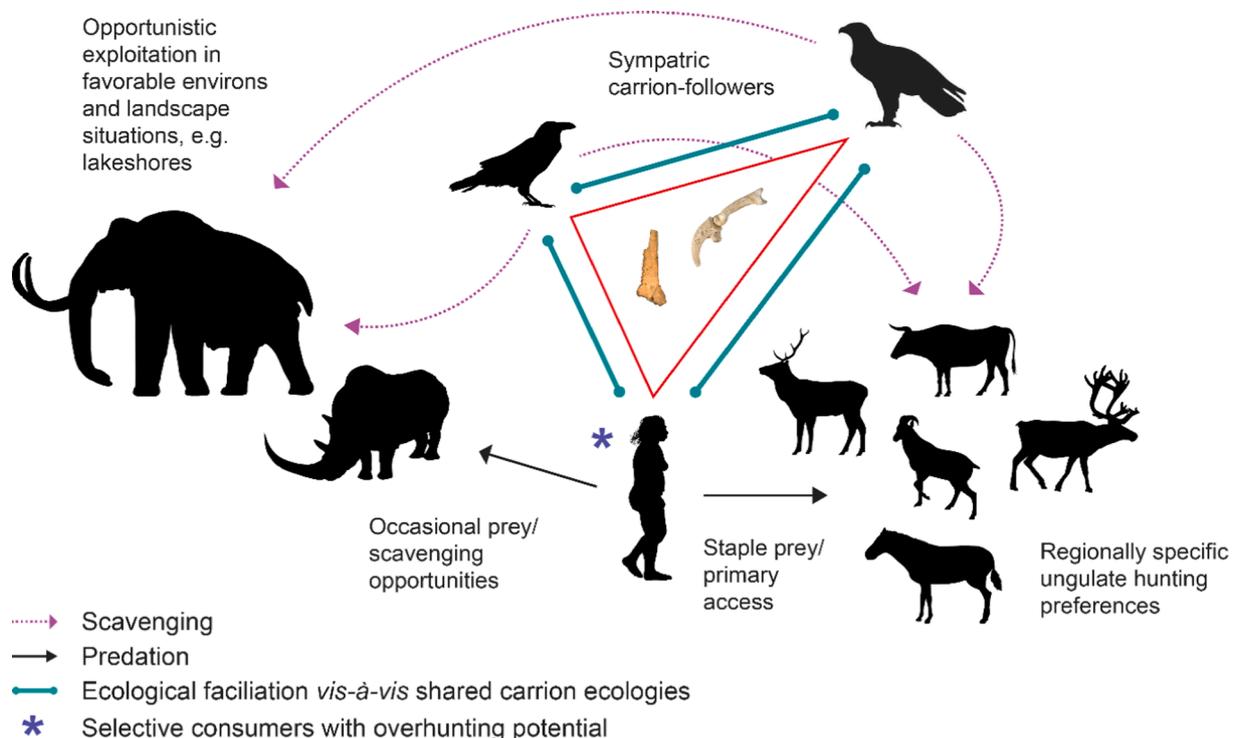
The accumulating evidence for Middle and Early Upper Palaeolithic, likely Neanderthal-associated, material engagement with raptors and corvids must therefore arguably be reframed as an emergent consequence of living and intersecting with these nonhuman others in the wider landscape and the resulting situational cross-referencing and interspecies attunement (Fig. 1). The extraction of raptor and corvid feathers (Peresani et al. 2011; Finlayson et al. 2012; Blasco et al. 2016; Romandini et al. 2016), the manipulation of raptor talons and their co-optation as bodily ornaments (Morin and Laroulandie 2012; Romandini et al. 2014, 2016; Radović et al. 2015; Rodríguez-Hidalgo et al. 2019; Laroulandie et al. 2020; cf., Table 1) as well as the modification of corvid bones (Majkić et al. 2017) can then be redressed as 'emergent materialities' of being and becoming Neanderthal in the carnivore and scavenger-invested animal ecologies of the early and middle Weichselian – and as such an inextricable part of evolving configurations of millennial-scale interspecies interaction and coordination. Ironically, this reframing of avian-related material culture in the Neanderthal

world draws attention to the importance of acknowledging and qualifying the uniquely derived intersection between different hominins and their animal surroundings, including the implied specificity of phenomenological references enveloped by the involved material culture, rather than perpetuating received interpretations construing the significance of these items in terms of cognitive capacity or Neanderthal 'behavioral modernity' (e.g., Peresani et al. 2011; Fiore et al. 2016; Frayer et al. 2020).

Finlayson et al.'s (2019) recent attempt to re-cast Neanderthal-raptor relationships as a 'cult of the Sun Bird' with strong culture-historical continuity claims based on direct parallels with practices of ethnohistoric groups in North America and elsewhere illustrates the pitfalls of such sapienscentrism. Finlayson et al. (2019) enthusiastically conclude that 'the long Human-Golden Eagle relationship may end up as the key example of the transmission of a symbolic-cultural behaviour from Neanderthals to Modern Humans'. While we agree with the assertion that hominin-raptor relationships were most likely culturally significant, we strongly caution against overly eager continuity propositions based on decontextualized analogies, naïve evolutionist and diffusionist premises as well as problematic understandings of culture and society as antipodes to 'nature', especially in the Pleistocene past where varying hominin biocultural dispositions are at play (cf., French 2019). Moving forward in the field of Pleistocene interspecies studies instead requires the careful calibration of archaeological interpretations with current multispecies theory and the comparatively assessable specificities and situated behaviors of hominins and animal others in their broader ecological and material contexts.

### 3.2. Hyenas: Neighbors who administer bodies

Pleistocene hyenas, as pointed out by Baynes-Rock (2015b), have customarily been studied in isolation from hominins (Kuhn 2011; Die-drich 2012, 2014, 2015), and their behavioral domains and ecosystem



**Fig. 1.** Tanglegram of salient ecocultural relationships between hominins, corvids and raptors in the Late Pleistocene landscape, and the 'emergent materialities' and practices interlaced with them. The red triangle represents the latent field of multispecies sociality which results from and shapes these interspecies relationships. Black outlines from <http://phylopic.org/> via the Public Domain; decorated raven bone (*Corvus corax*) from Zaskalnaya VI reproduced from Majkić et al. (2017: Fig. 3A); articulated eagle talons from Krapina reproduced from Radović et al. (2015: Fig. 6). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

impacts are deliberately re-cast as separate of the human, thus ironically prefiguring modes of behavioral hominin-hyena *rapprochement* primarily under the register of antagonism, conflict and competition (Brugal and Fosse 2004; Stiner 2004; Diedrich and Žák 2006; Villa et al. 2010; Enloe 2012; Dusseldorp 2011, 2013; Discamps 2014). This is astonishing given the well-documented, close ecogeographic association of early hominins and various hyena taxa throughout the Lower and Middle Pleistocene, especially in Africa (Turner 1990; Werdelin and Lewis 2005; Treves and Palmquist 2007). Even though the involved taxonomic groups change over time (Turner et al. 2008), *Hominidae* and *Hyaenidae* share an exceptionally long evolutionary history (Brantingham 1998; Stiner 2012), and either of the two is often a strong proxy for the presence of the respective other, as reflected in early expansions of faunal assemblages with hominins and hyenas from Africa into the Eastern Mediterranean and Western Europe (Arribas and Palmqvist 1999; Lewis and Werdelin 2010; Brugal et al. 2020), for example documented at key sites such as Dmanisi (Coil 2016), Pakefield (Parfitt et al. 2005; Iannucci et al. 2021) and Atapuerca (García and Arsuaga 2001).

Yet, this co-occurrence, and possible history of co-dispersal, has rarely been examined from a sympatric and sociocultural point of view – that is, in terms of coevolution in the above outlined sense – but mainly as a phenomenon of niche segregation and differentiation and the eventual competitive exclusion of the last hyenas in Late Pleistocene Europe (but *not* in Africa; cf., Stiner 2012; Galetti et al. 2018). Decentering of mutualities and more-than-hostile interstices between hominins and hyenas reflects the Western conviction of portraying biological organisms as ecologically ‘authentic’ as possible, which in the classic rendering is taken to call for a study of organisms ‘as they are by themselves’ (Baynes-Rock 2015a, 2015b), independently of other

interfering organisms (especially humans) and the adaptive ‘noise’ they produce. We suggest that the archaeological record of Late Pleistocene hominins other-than *H. sapiens*, in particular Neanderthals in Western Eurasia, therefore offers a useful model case to flip this received vision of the past on its head and begin exposing the evolved, intricate socially and materially productive, co-adaptive interfaces between hominins and their contemporary hyena neighbors in changing spatiotemporal contexts.

The ancestral cousins of today’s spotted hyenas (*Crocuta crocuta*) arrived in Europe shortly before 300 kya (Rohland et al. 2005; Turner et al. 2008), broadly falling into the second half of the Middle Pleistocene and thus predating ‘classic’ fossil Neanderthal phenotypes which only appear around MIS 5 (Serangeli and Bolus 2008). This timing bears evolutionary significance because what we recognize as Neanderthal biocultural characteristics developed gradually between ca. 350 and 300 kya, and thus in hyena-bearing ecosystems. Hyenas can even be considered to have been ‘superabundant’ in some of the ecologies mediating this process of ‘Neanderthalization’ (Turner et al. 2008; Galetti et al. 2018), with a possible palaeodemographic ‘Hyena event’ at the end of MIS 3 in Western Europe (Discamps 2009, 2014; see below). The combined archaeological and paleontological records clearly show that MIS 5–3 Neanderthals, especially in Western, Northwestern, Southern and Central Europe, consistently shared the landscape with these opportunistic and highly successful carnivores over many millennia (Fig. 2; Brugal and Fosse 2004; Arsuaga et al. 2011; Brugal et al. 2020). Neanderthals and hyenas also regularly used or at least visited the same localities, especially caves and other karstic landscape features, in temporal succession or not (e.g., Straus 1982; Brugal and Jaubert 1991; Villa and Soressi 2000; Villa et al. 2004; Beauval et al.

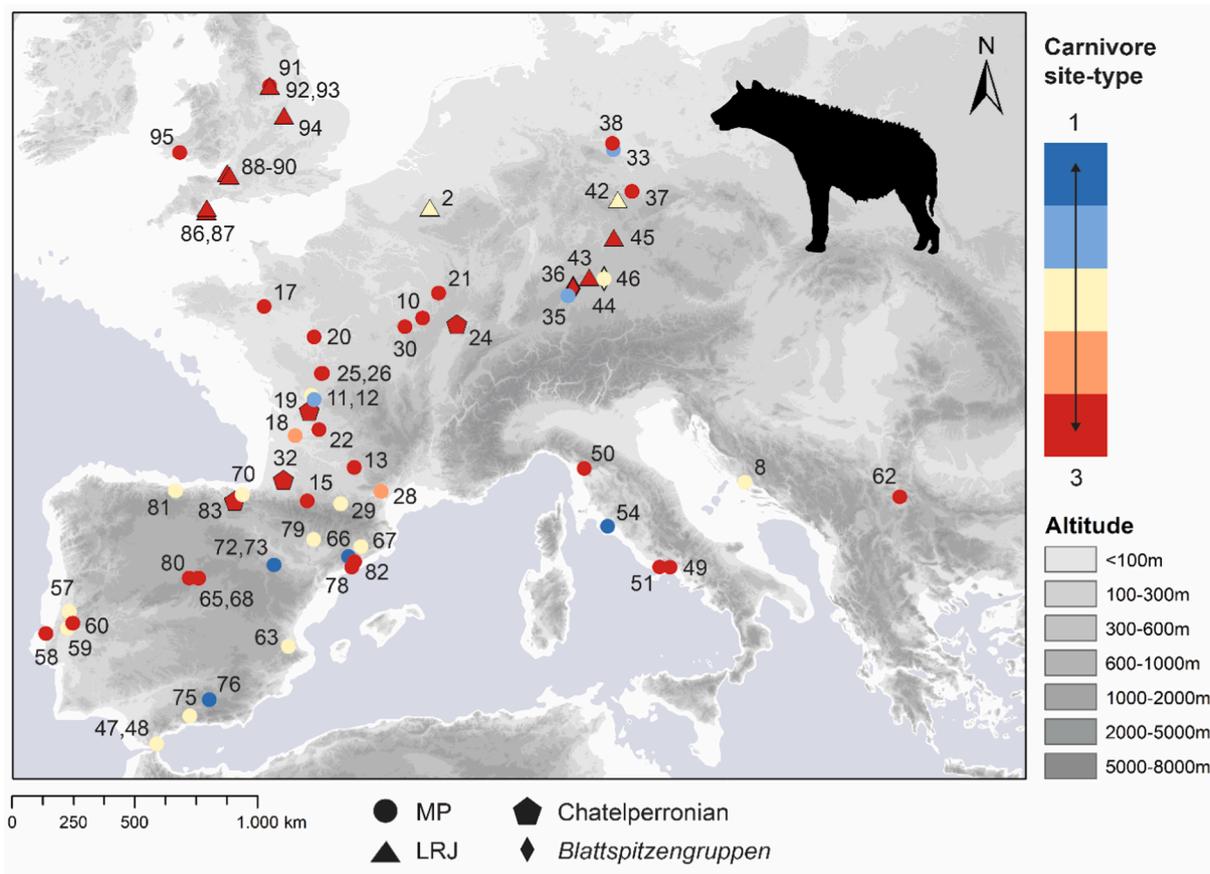


Fig. 2. Middle and incipient Upper Paleolithic sites with significant hyena input mentioned in the text and/or listed in Table 3 (site numbers correspond to site IDs in Table 3; Zaskalnaya VI and Matuzka are located outside of the shown map section). Colors indicate inferred site category and shape of symbols represent period/ techno-complex contexts (MP = Middle Paleolithic; LRJ = Lincombian-Ranisian-Jerzmanovician). Animal outlines from <http://phylopic.org/> via Public Domain.

2005; Miracle 2005; Brugal, 2010; Sala et al. 2012; Discamps et al. 2012; Turner et al. 2013; Morley et al. 2019). The quality of some of these sites as ‘persistent places’ (sensu Shaw et al. 2016; Maher 2021), furthermore, often derives from the space-altering activities of both agents and is to this effect ‘multispecies’ in nature. There are several reasons to believe that this notable spatiotemporal entanglement of Neanderthals and hyenas was not just a matter of self-confined geographic coexistence and fierce competition, but also implied heightened levels of interspecies immediacy and coordination with significant sociomaterial import, eventually leading to the development of ‘mutual ecologies’ (sensu Fuentes 2010; see above) which co-shaped the evolutionary trajectories of both hominins and hyenas.

First, the breadth of currently available evidence on hyena behavior in the present suggests that these animals are hyperflexible in their local adaptability and benefit from their pronounced ecological plasticity to make a successful living in varying environments and under shifting ecological regimes (Boydston et al. 2003; Abay et al. 2011; Mhlanga et al. 2017). After all, hyenas appear to be to a lesser extent adapted to specific conditions than to the exploitation of feeding opportunities that present themselves in different ecosystems, supported by their adept ‘cooperative problem solving’ (Drea and Carter 2009; Benson-Amram and Holekamp 2012) and mediated by multilevel, typically female-dominated clan-societies (Holekamp et al. 2012; Silk 2019; Ilany et al. 2021). In places where hyenas have survived until today, for example in the Horn of Africa, they have, in part because of their flexibility, almost always developed intricate relationships with humans and adapted to human-shaped environments (Gade 2006; Abay et al. 2011), to the point where hyena lifeways have become entirely dependent on their human neighborhoods (Baynes-Rock 2013, 2015a; Yirga et al. 2012).

Humans, in turn, have similarly adapted to their hyena neighbors, developing particular modes of relating and integrating hyenas into the cultural fabric of everyday life (Baynes-Rock 2015a). In the Harar region of Eastern Ethiopia, hyenas are for example bound up with human *khat* (*Catha edulis*) consumption and circulation, which the animals are thought to promote through their protective presence and often-overlooked pathogen clearing service (Fuentes and Baynes-Rock 2017). Hyenas are not only socially meaningful neighbors, who are involved in local identity formation and endow human stories and gossiping – i.e., so-called ‘hyena talk’ – as well as cultural understandings of landscape, they are sometimes deliberately fed close to or in human settlements (Baynes-Rock 2015a: 37) and as ‘caretakes’ of shrines and other important places receive special gifts to reaffirm human-hyena ‘commons’ (Baynes-Rock 2013), explicitly conceived as a form of ‘social contract’ (Baynes-Rock 2015a: 58-72). As Baynes-Rock (2016: 288) notes, the Harar data on human-hyena relations highlight that ‘people’s conceptual worlds are not so much constructed and structured within their minds as they are unfolded with Others in spatio-temporal, historically informed, phenomenal worlds.’

It is notable that human-hyena interstices seem to be particularly stable and culturally productive where humans rely to a large degree on animal products, especially meat, from medium to large-bodied ungulates (Baynes-Rock 2013: 215). Hyenas have plenty of feeding opportunities in these human-shaped contexts and at the same time provide valuable ecosystem services by taking care of carcasses, food scraps and residual bones. Even in settings with a less developed human fingerprint such as in protected areas, natural reserves or even national parks, hyenas adjust and synchronize their behavior in various ways with regard to human activities and exploit the few anthropogenic feeding opportunities that arise in these landscapes (Kolowski and Holekamp 2007), often at their outer fringes. Humans are therefore always an integral part of hyena ecologies, and this is probably also because hyenas have evolved in multispecies landscapes shared with hominins over thousands of years (cf., Moléon et al. 2014; Baynes-Rock 2015b). The mutualities of human-hyena relations and their proximate co-ecologies must consequently be re-considered also in their deep-time contexts.

The Neanderthal-hyena association in the European Late Pleistocene seems hardly coincidental then: Neanderthals were themselves powerful ecological keystone species and exhibited an elevated carnivorous profile (Richards et al. 2000; Bocherens 2011; Gaudzinski-Windheuser et al. 2018; Jaouen et al. 2019), even though plants and other food resources unquestionably also played a role in their diets (e.g., Hardy and Moncel 2011). Yet Neanderthals have been shown to consistently occupy the trophic apex of their ecological communities and to be capable big game hunters systematically targeting large-bodied mammals of up to 800-1000 kg (Uthmeier 2006), especially ungulates, even though their species preferences varied in space and time (Gaudzinski and Roebroeks 2001; Niven et al. 2012; Yravedra and Cobo 2015; Morin et al. 2016). The key point is that Neanderthals were among the landscape-scale carcass accumulators *par excellence* of their time, and Neanderthal presence certainly ensured the availability of predictable and specific types of carrion in the wider landscape. In contrast to later *H. sapiens* populations, Neanderthals, as noted before, also do not seem to have habitually exploited the entirety of animal carcasses and often selected only some of the available animal materials for further transformation (Patou-Mathis 2000: 393; Richter 2018: 202), often leaving behind for example the axial elements of the animals they killed (e.g., Valensi and Psathi 2004; Gaudzinski and Niven 2009) and in this way promoting a broad feeding niche especially for bone-cracking, osteophagic hyenas.

Based on their critical review of MIS 5–3 Neanderthal kill sites including Mauran, La Borde, Taubach, Zwölfen and Salzgitter-Lebenstedt, White et al. (2016) have furthermore shown that these hominins recurrently took advantage of opportune hunting situations and favorable topographic conditions, and often killed more ungulates than they excessively exploited (see also Daujeard et al. 2019) – they appear to have been fairly ‘discerning’ diners adding to the image of selective carcass processors and transporters discussed before. This behavioral proclivity would have facilitated hyena scavenging and simultaneously drawn hyenas and Neanderthals closer together in the landscape. Neanderthal sites with bone accumulations and evidence for secondary hyena interference are generally consistent with such a co-adaptive scenario (e.g., Majkić et al. 2018; Sanchis et al. 2019; Daschek and Mester 2020), now also supported by ZooMs findings, for example from Denisova cave (Brown et al. 2021), showing the chronostratigraphic importance of hyena activity, material accumulation and secondary bone modification and/or fragmentation at many Neanderthal sites across Eurasia. At Denisova, Morley et al. (2019) document near-continuous hyena occupation with a pervasive coprolite record and observe that ‘[s]pecific areas of the site might have been designated as waste dumps for lithic debitage and food detritus, [...], which in turn attracted scavengers such as the cave hyena when hominins were absent from the site.’

Secondly, broader MIS 5–3 Neanderthal land-use systems appear to have considerably overlapped with hyena core territories and den localities (Fosse 1997; Armand 1998; Stiner 2004; Dusseldorp 2013; Crezzini et al. 2016; Jimenez 2017), and *Crocota* places and hyena-invested locales seem to have regularly been integrated, although in complex and not always easy-to-decipher ways, into Neanderthal mobility patterns and land-use systems (Enloe et al. 2000; Villa and Soressi 2000; Villa et al. 2004, 2010; Huguet et al. 2010; Beauval and Morin 2010; White and Pettitt 2011; Discamps et al. 2012; Picin et al. 2020). Given the already noted territorial stability of Neanderthal groups inferred from eco-cultural niche models (Banks et al. 2021) and other lines of evidence indicating that Neanderthals frequently returned to the same places and sometimes valleys (cf., Wragg Sykes 2020: 216-218), we suggest that this interweaving of Neanderthal and *Crocota* geographies and the resulting mixing of hominin and hyena materialities (e.g., bones, artefacts) in particular landscape contexts, and often in recurrent fashion, reflects socioecological and landscape proximity between the two agents (cf., Jimenez et al. 2021: 2), thus pointing to situated modes of engaging with hyena others that were an integral part of Neanderthal society and culture. Hyenas co-defined the tracks,

pathways and rhythms typifying and binding together Neanderthal landscapes (pace Gamble 1998) and thus arguably co-shaped both the temporality and spatiality of hominin life in many parts of the Middle Palaeolithic.

Examples of such hybrid more-than-human landscapes and their interlaced Neanderthal-hyena geographies are not difficult to pinpoint in the European Middle Palaeolithic. In the Bohemian karst and the area surrounding Prague, for example, a dense lineup of caves and palaeoravines with evidence for pronounced hyena activity (Diedrich and Zák 2006) meets broadly penecontemporaneous but relatively sporadic hominin presence with only a few sites such as Bečov documenting more extensive Neanderthal occupation, while many other Middle Palaeolithic sites have yielded only a handful of lithic artefacts (Valoch 2013a), either associated with hyena contexts or not. The Sauerland karst region in Western Germany similarly documents microregional overlay of major Neanderthal occupation sites such as Balve cave (Kindler 2012) and Volkringhauser Höhle (Tafelmaier 2011) and intense hyena denning activity, for example well-attested at Perick caves and Wilhelms cave (Diedrich 2009, 2011). Another example is Southwestern France where diversified Neanderthal settlement occurs within rich hyena landscapes (Discamps 2011), including a large number of penecontemporaneous den sites such as Plumettes, Camiac and La Chauverie, some of which have yielded small numbers of lithic artefacts and human-modified bones in dense hyena-accumulated deposits (Discamps et al. 2012; Airvaux et al. 2012). A final example is provided by the Belgian Ardennes where a cluster of important Late Middle Palaeolithic sites including Spy, Scladina, Walou and Goyet, in which the majority of human-accumulated faunal assemblages were also affected by subsequent hyena activity (Daujeard et al. 2016), are found in direct spatial proximity to the recently identified long-term hyena birthing den of Caverne Marie-Jeanne, dated to the same narrow MIS 3 timeframe as the adjacent Neanderthal sites (Jimenez et al. 2021). Interestingly, cementum analysis of teeth from hyenas and their prey from the latter region has detected a marked absence of seasonal differences in occupation, suggesting that hyena populations were firmly established in, and regionally attached to, the Belgian Ardennes (Jimenez 2017). All of this suggests that hyenas were familiar co-inhabitants and spatial ‘companions’ (pace Haraway 2007) as well as key configurators of Neanderthal lived experience in various European regions.

A critical review of the European Neanderthal record further indicates that there are at least three different types of archaeological sites which can be discriminated in order to elucidate the dynamics of hominin-carnivore engagement (Table 2), and all three site types appear to have been a common component of Neanderthal land-use systems, spatial understanding and ‘landscaping’ (pace Arroyo-Kalin 2016), even though not all of them were necessarily of equal importance for different Neanderthal groups at different times and in different regions (cf., Fig. 2):

- ‘Type one’ sites encompass archaeological occurrences where material culture is abundant and hominins appear to have been the primary agents of site formation and material accumulation but subordinate carnivore activity is sometimes also attested.
- ‘Type two’ sites comprise archaeological occurrences in which Neanderthal material culture is frequent but carnivore behaviors and remains have also contributed substantially to the formation and nature of the deposits; these sites often document alternate frequentation of hominins and other carnivores, including Pleistocene hyenas.
- ‘Type three’ sites are characterized by the anecdotal presence of hominin material culture, often only a few selected items such as finished and curated lithic tools, and carnivores are the primary formative agents; these sites sometimes bear partial hominin skeletal remains or isolated bones and teeth (e.g., Tournepiche 1994; Stiner 1991, 1994; Beauval et al. 2005; Enloe 2012; Diedrich 2014; see

**Table 2**

Three-tiered categorization of archaeological sites with implications for understanding carnivore neighborhoods and hominin-carnivore intersections in different palaeolandscapes.

Site category	Signature(s)
1	Hominin material culture is abundant and operational sequences tend to be complete; important role of local raw materials and their on-site transformation/consumption; artefact-bearing layers are primarily anthropogenic in nature; reduced evidence of carnivore bone interference; primary access of carcasses by hominins; pronounced spatial organization of hominin activities and evidence for repeated or longer-duration stays
2	Hominin material culture is frequent but operational sequences are fragmented; carnivore remains are frequent and carnivores have substantially contributed to bone accumulation and archaeological site-formation; non-local raw materials and the import of finished and/or curated tools or cores play more important roles; elevated frequencies of gnawing and bite marks; often but not always alternate frequentation of hominins and carnivores; ephemeral/short-term hominin occupations
3	Hominin material culture is anecdotal or extremely rare and only specific items (e.g. bifacial tools) or fragmented/isolated hominin fossils are found; incomplete operation sequences with emphasis on the distal segments; evidence for carnivore habitation/denning/hibernation, e.g. abundant coprolites; elevated ratio of juvenile individuals among bones and teeth (including presence of cubs), >10 % gnawing mark frequency; evidence for primary access of carnivores to at least some animal carcasses; burrows or other animal habitation, hibernation and feeding structures; ephemeral/short-term hominin occupation or ‘visitation’ signatures

discussion below) and frequently correspond to carnivore habitation sites such as hyena dens.

The three site-types are distinguished by a differential contribution and mixture of behavioral and material signatures of hominins and hyenas. This interweaving of hominin and hyena spatialities again reassures us of the geosocial proximity between the two and that they were differentially engaging with each other not only in the open landscape but in different landscape situations and with reference to different kinds of places with varying degrees of hominin and hyena ‘authorship’, even though time averaging, taphonomic filtering, occupational histories and the details of site formation need to be carefully considered on a case-to-case basis. This complex and spatially differentiated pattern of hominin-hyena exposition involved hominin visitations of hyena occupation sites (cf., Airvaux et al. 2012; Rodríguez-Hidalgo 2010; Discamps et al. 2012; Picin et al. 2020: 3), and the other way around, for example when hyenas had secondary access to otherwise anthropic faunal accumulations (e.g., Costamagno et al. 2005; Daschek and Mester 2020) and possibly ravaged Neanderthal deposits and fossil remains (Diedrich 2014). Direct evidence of two butchered hyena remains within the otherwise nonhuman-accumulated deposits from the depths of Maltravieso cave in Southwestern Spain broadly dating to MIS 5 indicates that the exploration and potential scouting of hyena-infused places has an extended history at least among some Neanderthal groups (Rodríguez-Hidalgo 2010).

All of this supports a potent co-adaptive nexus of Neanderthals and hyena others and highlights that the associated interspecies neighborhoods mattered a great deal, steering and variously co-configuring hominin behaviors and ‘horizons of concern’ (pace Bird-David 2017a). The affirmation and reproduction of ‘mutual ecologies’ (pace Fuentes 2010) was thus perhaps a more important factor in shaping Neanderthal spatial organization and landscaping than previously acknowledged. The mixing of Neanderthal and hyena materialities in different locations in the landscape may accordingly not only tell us something about the nature and scheduling of subsistence-related tasks, but also reflect ongoing negotiations of place and the significance of sharing the landscape with nonhuman carnivores. Given that movements and material

traces in the landscape can be viewed not only as physical concretizations of past behaviors but equally as residues or flows of knowledge (McBryde 2000; Rockman 2013), Neanderthals were apparently concerned with acquiring hyena-related landscape knowledge, to learn about hyena places and to familiarize themselves with these proximate carnivores, so that hyena spatialities would figure prominently in Neanderthal social memory.

The deliberately incised fragment of a hyena femur from Les Pradelles in Southern France (d'Errico et al. 2018) – a 'type one/two' site dating to MIS 4 – provides an intriguing example of material engagement with hyenas as important landscape co-dwellers, and can be re-interpreted as a form of 'emergent materiality' within socio-ecologically meaningful, yet nevertheless precarious hominin-carnivore neighborhoods. The incised hyena femur makes its appearance in layer 2a of Les Pradelles, which has been interpreted as a specialized Quina Mousterian reindeer hunting and processing station with considerable hyena input (Costamagno et al. 2005, 2006). The site also yielded an unusual assortment of intensively processed Neanderthal body parts, originally belonging to at least 9 individuals (Wragg Sykes 2020: 303). Interestingly, the condition of the hominin bones is much more heterogeneous than the associated primary anthropogenic ungulate fauna, and a major hominin concern was body and bone fragmentation, and perhaps export, as indicated but the unequal representation of hominin body parts (Mussini 2011), also documented in other Middle Palaeolithic sites with excessive hominin-oriented body manipulation such as Krapina, Moula-Guercy and El Sidrón (cf., Wragg Sykes 2020: 300-307). Not only does this treatment structurally mimic the carcass ravaging and bone-cracking behavior of hyenas, there is also evidence for hyena consumption of hominin teeth as well as considerable hyena-induced damage on hominin bones themselves (Maureille et al. 2017).

Even though it is not entirely clear whether the marked hyena femur is of local origin or was imported to the site, both hyenas and Neanderthals had some kind of access to each other's bodies, and the broader context of layer 2a evokes the fluidity and permeability of hominin-hyena interstices involving material exchange and mutual body transformation, which not only created a mingled multispecies assemblage but also links the biography of hominin remains to place-bound hyena agency, highlighting the world-making capacity of these nonhuman carnivores. Moreover, Les Pradelles is one of the few Middle Palaeolithic sites where hominin bones were selected and co-opted as retouchers and the respective bones are robust femur shaft fragments (Rougier et al. 2016; Costamagno et al. 2018b), and thus, analogically speaking, reference the same body part as the marked hyena femur found at the site. The incised hyena bone from Les Pradelles, we would argue, has to be understood against the larger background of this complex reticulation of human and nonhuman materialities and associations. As Wragg Sykes (2020: 303) has pointed out, there is good reason to conceive of the involved behaviors as 'acts of intimacy, not violence' and this point can be nuanced by taking stock of the broader hominin-animal-material interrelationships and material exchanges and transformations implicated at Les Pradelles. Interpreting the marking of the hyena femur as 'emergent materiality' of specific place-bound Neanderthal-hyena intersections has the advantage of recognizing the situational context of human and nonhuman agencies and references as a key motivation for the observed material engagement, without overrating (or underrating) the idiosyncrasy of the object in question.

In addition, Les Pradelles draws attention to larger ecosystem dynamics during MIS 4 – the heyday of the Quina Mousterian (Jaubert et al. 2011; Faivre et al. 2017) – when the total herbivore biomass in Southwestern France seems to have decreased (Discamps 2014) and large ungulate herds would have been focal landscape agents and carnivore attractors. The apparent specialization of Quina Neanderthals on reindeer groups and their strategic interception resulting in extensive, spatially dense bone dumps would have thus acted as particularly strong magnets for hyena mobility and consumptive activity, with the interesting possibility of at least partial specialization in the predictable

exploitation of Neanderthal hunting leftovers. Neanderthal sites like Les Pradelles and Jonzac document the recurrent use of certain locales for reindeer processing by hominins and include evidence for non-comprehensive carcass treatment during the Quina Mousterian (Costamagno et al. 2006; Niven et al. 2012). The mixing of Neanderthal and hyena signatures at these places would have thus created a powerful background for distributed, multispecies place-making, where hominins and hyenas were not only drawn together but co-created the defining sense, experience and signification of place through mutually reinforcing actions. It is this special association of 'Neanderthal-ness' and 'hyena-ness' that arguably crystallizes in the incised hyena femur from layer 2a.

In Western Europe, especially in France (e.g., Brugal and Jaubert 1991; Airvaux et al. 2012; Discamps et al. 2012), Germany (e.g., Müller-Beck 1968; Hülle 1977; Böttcher et al. 2000; Uthmeier et al. 2018) and on the Iberian peninsula (e.g., Rodríguez-Hidalgo 2010; Brugal et al. 2012; Picin et al. 2020), there is also growing evidence for Neanderthal ventures into 'domestic' hyena spaces as indicated by 'type three' sites with a reduced hominin fingerprint, often associated with hyena maternity dens with plenty of coprolites and youngster-dominated mortality profiles (cf., Table 2, Table 3). For instance, localities interpreted as important hyena dens or hideouts in Spain such as Cueva del Camino (Arsuaga et al. 2012), Cueva de la Buena Pinta (Huguet et al. 2010) or Portalón del Tejadilla (Sala et al. 2020) have yielded sparse evidence for hominin presence, often a few isolated lithic artefacts only. A cut-marked lynx humerus with superimposed carnivore toothmark from the hyena den of Cueva de la Zarzamora may also result from Neanderthal excursions into hyena living grounds, even though other interpretations are also possible (Sala et al. 2012). In Iberia, hyenas generally became hyperubiquitous carnivores at the end of the Middle Palaeolithic (Sauqué et al. 2017) and the tightened intersection of hominins and hyenas documented there archaeologically is thus perhaps also a consequence of this emerging ecological salience (Daura et al. 2017; Picin et al. 2020).

Practices of visiting hyena spaces and their varying material correlates can be viewed in connection to the special importance of hyenas as landscape agents and proximate neighbors. Visiting alien spaces 'stained in hyena' may then, generally speaking, express *situated strategies of relating* to hyena others, affirming and reproducing lived ecocultural adjacency and propinquity – and this holds independently of whether or not hominin presence was concomitant with hyena den occupation or not since hyena-stained places can be understood as part of the extended phenotype and personhood of hyenas in a wider, shared landscape. In a similar vein as Politis (1996) has argued that human foragers 'move to produce', we consequently suggest that Neanderthals may in part have 'moved to relate', and some nodes in their mobility networks can thus probably be re-examined as interspecies 'contact zones'. This mode of relating to hyena others arguably points to a broader ethos of sharing that goes beyond mere resource competition and antagonism, indicating that hyenas participated in the larger social field of hominins and were recognized as significant others, perhaps even *persona* (Fig. 3). Rather than contradicting with, this explicitly encompasses practical uses of hyena dens as part of the 'giving environment' (pace Bird-David 1990), serving as valuable faunal caches (cf., Discamps et al. 2012) and thus facilitating the acquisition of specific, thought-after animal bones and body parts. In modern-day India, for instance, scavengers facilitate the collection of high-quality cattle bones since they efficiently clean the animals' carcasses and make them readily available, thereby providing important 'cultural ecosystem services' (Markandya et al. 2008).

Bradley's (2000) arguments on the importance of landscape biography and 'natural' places in the making and evolution of human landscapes are also worth recalling here. The frequently encountered occupational sequence of alternating habitations of hyenas and Middle Palaeolithic hominins, often beginning with hyena denning activities followed by more-or-less structured hominin domestic use of space (e.g., Spagnolo et al. 2020) may then be positively turned – as reasserting

**Table 3**

Selected archaeological sites from Western, Central and Southern Europe dated to between MIS 5 and 3 with evidence for different modes of co-habitation among hominins and hyenas or bears. Sites are classified according to the criteria listed in Table 2 (MP = Middle Paleolithic; LRJ = Lincombian-Ranisian-Jerzmanovician; UP = Upper Palaeolithic). Sites are mapped in Figs. 2 and 4.

ID	Site name	Layer	Country	Period	Marine Isotope Stage	Site category	Focal carnivore context (hyena/bear)	Number of lithic artefacts	Reference(s)	
1	Walou	CV2, C18	Belgium	MP	MIS 5–3	2	Bear	ca. 1500 lithics in 2 levels, including Mousterian points, MTA bifaces and foliates	<a href="#">Di Monica et al. 2013</a> ; <a href="#">Daujeard et al. 2016</a>	
2	Spy	Lower (Mousterian) to Middle or Intermediate Fauna-bearing Level (FBL) (Aurignacian/Mousterian with leaf points): “Deuxième and Troisième niveau ossifère”	Belgium	MP/LRJ	MIS 3	2	Hyena?	Second Fauna Level	>1000 lithics, including 25 blade points (only a small subset including the blades are safely attributed to the LRJ)	<a href="#">Flas 2013</a> ; <a href="#">Germonpré et al. 2013</a> ; <a href="#">Semal et al. 2013</a>
3	Goyet	Second Fauna Level	Belgium	LRJ	MIS 3	3?	Bear	3 blade points, 1 endscraper	<a href="#">Flas 2013</a> ; <a href="#">Peigné et al. 2009</a>	
4	Scladina	1A	Belgium	MP	MIS 3	2	Bear	ca. 4500 lithics associated with Levallois, Discoid and Quina production	<a href="#">Di Monica 2010</a> ; <a href="#">Abrams et al. 2014</a> ; <a href="#">Daujeard et al. 2016</a>	
5	Bacho Kiro	Layer I	Bulgaria	IUP	MIS 3	1	Bear	ca. 1500 lithics with laminar blade technology and Levallois-like point production (ca. 30% of the assemblage is retouched, with an emphasis placed on blade points)	<a href="#">Hublin et al. 2020</a>	
6	Zaskalnaya VI	III	Crimea	MP	MIS 3	1	other	>900 lithics, including Micoquian bifacial tools of “Ak Kaya Tradition” and flat, sub-parallel core technology (high tool ratio)	<a href="#">Majkić et al. 2017</a>	
7	Krapina	9 MP levels	Croatia	MP	MIS 5	2?	Bear	1191 lithics in 9 layers, dominated by sidescrapers with river cobble exploitation	<a href="#">Karavanić 2004</a>	
8	Mujina Pecina	D1, D2	Croatia	MP	MIS 3	2	Hyena/bear	222 lithics associated with Levallois production; small tools including blade component, points, backed knives and foliates (ca. 50% of the artefacts are tools)	<a href="#">Miracle 2005</a> ; <a href="#">Karavanić et al. 2008</a>	
9	Vindija	G1	Croatia	MP/Szeletian/UP	MIS 3	3	Bear	ca. 10–20 lithics, mainly tools with bifacial points made of exogeneous raw materials, a prismatic bladelet core and organic split-based points	<a href="#">Miracle et al. 2010</a> ; <a href="#">Zilhão 2009</a>	
10	Grotte de la Roche aux Chats		France	MP	MIS 5–4?	3?	Hyena	ca. 40 lithics including plain débitage and simple points as well as heavy-duty implements	<a href="#">Joffroy et al. 1959</a>	
11	Artenac	Couches 10–8	France	MP	MIS 5–4?	2	Hyena/bear	ca. 16,000 lithics (centripetal Levallois with scrapers and bifaces followed by a Ferrassie Mousterian)	<a href="#">Delagnes et al. 1999</a>	
12	Les Pradelles/Marillac	Facies 2a	France	MP	MIS 4	1/2	Hyena	444 lithics including Quina products and sidescraper-rich toolkit	<a href="#">Frouin et al. 2017</a> ; <a href="#">Costamagno et al. 2006</a>	
13	Peyre II	Couche 4	France	MP	MIS 5?	3	Hyena			

(continued on next page)

Table 3 (continued)

ID	Site name	Layer	Country	Period	Marine Isotope Stage	Site category	Focal carnivore context (hyena/bear)	Number of lithic artefacts	Reference(s)
14	Grotte de Preletang		France	MP	MIS 5?	3	Bear	2 lithics (pseudo-Levallois flake and simple scraper)	Brugal and Jaubert 1991; Fourvel et al. 2012
15	Grotte de la Carrière	Couche E	France	MP	MIS 5/4?	3	Hyena	164 lithics, mainly pseudo-Levallois points and scrapers	Brugal and Jaubert 1991
16	Ramandils	Unit II	France	MP	MIS 5	2		<10 lithics in a hyena den with “discoidal” core and single scraper	Clot 1970
17	Grotte aux Ours de Châteaubourg	Ensemble B	France	MP	MIS 4?	3	Hyena/bear	8380 lithics; simple débitage with small tools	Rusch et al. 2019
18	Camiac		France	MP	MIS 3	2/3	Hyena	ca. 50 lithics including a Levallois core and classic Mousterian tools	Pautret-Homerville et al. 2011
19	La Chauverie		France	MP/ Chatelperronian	MIS 3	3	Hyena	186 lithics with Discoid production, plain flakes and scrapers	Discamps et al. 2012
20	La Roche-Cotard II		France	MP	MIS 3	3?	Hyena	54 lithics including unidirectional Levallois products and bifaces (plus a single Chatelperronian point)	Discamps et al. 2012
21	Perthuis de Roche		France	MP	MIS 3	3?	Hyena	Low lithic count including Levallois products and large scrapers	Marquet 1999
22	Cassénade	Couche 2	France	MP	MIS 3	3	Hyena/bear	9 lithics, mostly heavily retouched tools and a biface of “Micoquian” affinity	Mouton and Joffroy 1948
23	Cassénade	Layer 2 main sector	France	IUP	MIS 3	3?	Hyena	>100 lithics with diverse productions, bifacial technology and pseudo-Levallois points	Discamps et al. 2019
24	Fouvent (Abri Cuvier)		France	MP/ Chatelperronian	MIS 3	3	Hyena	>200 lithics including 6 Chatelperronian points and diverse blade tools mounted on laminar blanks	Discamps et al. 2019
25	Plumettes	Niveau inférieur (IV) and supérieure (II)	France	MP	MIS 3	3	Hyena	ca. 300 lithics including cores, tools and splinters interspersed within four palaeontological horizons	Fourvel et al. 2012, 2015
26	Rochers-de-Villeneuve	Niveau supérieure (J) and moyen (N)	France	MP	MIS 3	3	Hyena	ca. 60 lithics including Levallois products with large scrapers and unipolar laminar production; inversely retouched bladelet and broken Chatelperronian point	Beauval and Morin 2010; Discamps 2011; Airvaux et al. 2012
27	Le Figuier		France	MP	MIS 3	2	Bear	ca. 700 lithics including Levallois products with large scrapers followed by a Denticulated Mousterian assemblage with Discoid production	Moncel et al. 2012; Daujeard et al. 2016
28	Tournal	Couche à Ours	France	MP	MIS 3	2/3	Hyena	ca. 730 lithics with Discoid and Levallois production and low tool ratio	Tavoso 1987; Marín et al. 2020
29	Portel Ouest	F2	France	MP	MIS 3	2	Hyena	1579 lithics with Discoid and Levallois production	Jaubert 1993; Becam and Chevalier 2017
								>10000 lithics (Quartzite-rich Mousterian with important bifacial component and almost 500 tools, but no formal	

(continued on next page)

Table 3 (continued)

ID	Site name	Layer	Country	Period	Marine Isotope Stage	Site category	Focal carnivore context (hyena/bear)	Number of lithic artefacts	Reference(s)
30	Grotte du Bison (Arcy-sur-Cure)	Level I	France	MP	MIS 3	3?	Hyena/bear	Levallois and/or Discoid production) ca. 20 lithics	Enloe 2012
31	Grotte du Bison (Arcy-sur-Cure)	Level D	France	MP/ Chatelperronian	MIS 3	2	Bear	>200 lithics	Enloe 2012
32	Brassempouy (Grotte du Pape)		France	MP/ Chatelperronian	MIS 3	3?	Hyena	Low lithic count including laminar products and 13 Chatelperronian points	Buisson and Delporte 1990
33	Königsau	A, B	Germany	MP	MIS 5	1/2	Hyena?	>5000 lithics including bifacial tools	Mania and Toepfer 1973; Hedges et al. 1998; Picin 2016
34	Grosse Grotte	III-XI	Germany	MP	MIS 4/3?	2?	Bear	>900 lithics in 9 layers	Conard et al. 2012
35	Kogelstein	AH0, AH1o, AH1u, AH2	Germany	MP	MIS 4/3	2/3	Hyena	ca. 450 lithic distributed over 4 layers (between 2 and 243 artefacts per layer), including bifacial tools and <i>Keilmesser</i>	Böttcher et al. 2000
36	Haldenstein	h	Germany	MP/ <i>Blattspitzengruppen</i>	MIS 3?	3	Hyena/bear	3 lithics (2 leaf points and a large blade)	Riek 1938; Conard et al. 2012
37	Lindenthal Hyena Cave		Germany	MP	MIS 3?	3	Hyena	38 lithics including 4 bifacial backed knives (but: not all artefacts are MP and there is probably younger input as well)	Liebe 1876; Mania and Toepfer 1973
38	Westeregeln		Germany	MP	MIS 3?	3	Hyena	1 bifacial backed knife, 1 handaxe	pers. com. Th. Weber
39	Sirgenstein	VII/VIII	Germany	MP	MIS 3	2?	Bear	704 lithics with Levallois and Discoid production; imported Quina scrapers and Levallois points (high core ratio and high curation index)	Conard et al. 2012; Bertacchi et al. 2021
40	Einhornhöhle	4.5	Germany	MP/UP	MIS 3	3	Bear	1 bladelet	Leder et al. 2021
41	Ranis	XI	Germany	MP	MIS 3	2	Bear	16 lithics including 1 bifacial point, 1 bifacial tool and 14 plain flakes	Hülle 1977
42	Ranis	X	Germany	LRJ	MIS 3	2	Hyena/bear	63 lithics including 24 blade points and 19 bifacial points	Hülle 1977; Grünberg 2006; Higham et al. 2007
43	Schmähingen		Germany	LRJ	MIS 3	3	Hyena	3 blade points and 1 blade	Uthmeier et al. 2018
44	Weinberghöhlen (Mauern)	F ("Zone 4")	Germany	<i>Blattspitzengruppen</i>	MIS 3	2	Hyena/bear	398 lithics (high tool ratio: 111 tools, including many leaf points and 2 handaxes)	von Königswald and Müller-Beck, 1975; Richter 2009; Kot and Richter 2012
45	Zwergloch (Pottenstein)		Germany	LRJ	MIS3?	3	Hyena?	1 typical Jerzmanovice point and a few unmodified artefacts	Birkner 1915; Müller-Beck 1968; Flas 2008
46	Weinberghöhlen (Mauern)	G, H, I ("Zone 5")	Germany	MP	MIS 3	2	Hyena/bear	609 lithics with 89 tools, including leaf points, handaxes and bifacial knives	von Königswald and Müller-Beck, 1975; Richter 2009; Kot and Richter 2012
47	Vanguard Cave	C-D units, Levels 9–22	Gibraltar	MP	MIS 5–3	2	Hyena	343 lithics in a 17 m stratified sequence; Discoidal core technology with many retouched tools, including simple flake tools and double side-scrapers	Carrión et al. 2018; Barton et al. 1999; Barton 2012
48	Gorham's Cave	IV	Gibraltar	MP	MIS 3	2	Hyena	202 lithics; preferential Levallois production with points; tools	Pacheco et al. 2012; Carrión et al. 2008;

(continued on next page)

Table 3 (continued)

ID	Site name	Layer	Country	Period	Marine Isotope Stage	Site category	Focal carnivore context (hyena/bear)	Number of lithic artefacts	Reference(s)
49	Moscerini	M5	Italy	MP	MIS 5/4?	3?	Hyena	predominantly sidescrapers and some denticulates	Stiner 2004
50	Buca della Iena	I1-2	Italy	MP	MIS 4/3?	3	Hyena	127 lithics	Stiner 2004
51	Grotta Guattari	G0	Italy	MP	MIS 4/3	3	Hyena	35 lithics	Stiner 2004
52	Rio Secco	5, 7, 8	Italy	MP	MIS 3	2/3	Bear	2 scrapers with Quina retouch	Romandini et al. 2018; Peresani et al. 2014
53	Fumane	A5-A6	Italy	MP	MIS 3	1	Bear	104 lithics in 4 levels with high point ratio but also notched pieces and "limaces", together with Discoid as well as elongated recurrent-centripetal Levallois production (but very low core ratio)	Jéquier et al. 2012; Peresani et al. 2011; Peresani 2012
54	Grotta di Santi	Floor 105A	Italy	MP	MIS 3	1	Hyena	>2000 lithics with Levallois production and many scrapers	Spagnolo et al. 2020
55	Nietoperzowa Cave	6, 5, 4	Poland	LRJ	MIS 3	2?	Bear	116 lithics with only a few tools; Levallois and unidirectional volumetric production (many tools are imported as finished products)	Krajcarz et al. 2018; Flas 2008
56	Koziarnia Cave		Poland	MP/LRJ	MIS 3	2	Bear	50 lithics in 3 levels, including many blade points and bifacial points	Flas 2008; Chmielewski et al. 1967; pers. com. M. Kot
57	Buraca Escura	US3	Portugal	MP	MIS 5/4?	2	Hyena	1 blade point and Late Middle Palaeolithic artefacts, including bifacial backed knives	Arcerredillo et al. 2018
58	Furninha	Bonebed 3 to bonebed 8	Portugal	MP	MIS 4-3	3	Hyena	39 lithics with recurrent-centripetal Levallois, Discoid and Kombewa productions	Brugal et al. 2012; Bicho and Cardoso 2010
59	Gruta da Oliveira	The Mousterian Cone, Layer 19 to layer 8	Portugal	MP	MIS 3	2	Hyena	37 lithics; bone bed 3 is the most abundant find context (MIS4/80.000 BP) and includes, e.g., a biface	Zilhão et al. 2010; Trinkaus et al. 2007
60	Cueva de Caldeirão	levels Q-L	Portugal	MP	>MIS 3/2	3	Hyena	95 lithic (>2.5 cm, mainly layer 14 and 13); Levallois flake production; few formal tools including notches, denticulates and irregularly retouched blanks	Lloveras et al. 2011; Zilhão et al. 2021
61	Matuzka	5, 6, 7	Russia	MP	MIS 5-4?	2/3	Bear	87 lithics in total in the Mousterian layers (L to Q), including a single core, flakes, chips and two retouched tools	Hoffecker and Cleghorn 2000
62	Pešturina	4	Serbia	MP	MIS 3	3	Hyena	127 lithics from 3 layers (high tool ratio)	Majkić et al. 2018
63	Cova Negra	Level XV (MIS5e), X-XIII (MIS5b-d), XII (MIS5a), V-XI (MIS4-3), IV (Würm Interstadial II-III), I-III (MIS3/MIS2 UP and mixed Mousterian)	Spain	MP	MIS 5-3	2	Hyena	47 lithics with sidescrapers, notches and denticulates (low core ratio)	Arsuaga et al. 2007; Villaverde et al. 1996

(continued on next page)

Table 3 (continued)

ID	Site name	Layer	Country	Period	Marine Isotope Stage	Site category	Focal carnivore context (hyena/bear)	Number of lithic artefacts	Reference(s)
64	Arlanpe	Level D	Spain	MP	MIS 5	1	Bear	(plus low cortical representation) >50 stone tools>20 mm per sqm	Arcercedillo Alonso et al. 2013
65	Cueva del Camino	Level 5	Spain	MP	MIS 5	3	Hyena	105 lithics, 52 from level 5; predominantly quartz artefacts; only a few cores and retouched pieces	Arsuaga et al. 2012; Hugué et al. 2010
66	Abric Romani	A, B (top of the profile)	Spain	MP	MIS 4–3	1	Hyena	> 10,000 lithics (e.g., level J=>5000 lithics, level M = 6083 lithics, level P = 2633 lithics)	Marín et al. 2017; de Soler et al. 2020
67	Cova de Teixoneres	sub-unit IIIb-IIIa	Spain	MP	MIS 4–3	2	Hyena < 7bear	>3000 lithics (sub-unit IIIb = 3314 lithic, sub-unit IIIa = 500 lithics)	Picin et al. 2020; Álvarez-Laó et al. 2017
68	Cueva de la Buena Pinta	Level 2 to 5	Spain	MP	MIS 4–3	3	Hyena	Small assemblage of flakes made of flint and quartz	Hugué et al. 2010
69	Cova Eirós	Level 3 and level 4	Spain	MP	MIS 4	2	Bear	>700 from level 3 and 4 (level 4 is the most find-rich); only a few cores with longitudinal/orthogonal exploitation strategies and some Discoidal and Levallois production; some retouched tools on flakes (sidescrapers, denticulates); final stage reduction (low cortical piece count)	de Lombera-Hermida et al. 2014
70	Cueva de Amalda	Nivel VII	Spain	MP	MIS 3–2	2	Hyena/bear	>1000 lithics, including ca. 200–300 tools; Kombewa, Levallois and bifacial production.	Terreros (2007); Rios-Garaizar 2010
71	Abauntz	Niveles G and H	Spain	MP	MIS 3	3	Bear	42 lithics and burned bones from Mousterian level H; 11 cleavers, two handaxes, two sidescrapers, two endscrapers, three truncations and four retouched flakes	Utrilla et al. 2015; Altuna et al. 2001
72	Aguilón P7		Spain	MP	MIS 3	3	Hyena/bear	1 lithic artefact (simple convex scraper with Quina retouch)	Sauqué et al., 2014; Mazo and Alcolea 2020
73	Aguilón P5	cnc, mcp and e	Spain	MP	MIS 3	1	Hyena	>2000 lithics (level cnc = 367 lithics, level mcp = 1700 lithics, level e = 125 lithics); scrapers, notches, denticulates, naturally-backed knives, non-retouched tools, flakes and retouched laminar blades	Mazo and Alcolea 2020
74	Amutxate		Spain	MP	MIS 3	3	Bear	4 lithic artefacts recovered during excavation	Torres et al. 2007
75	Boquete de Zafarraya	UB, UC, UD, UG	Spain	MP	MIS 3	2	Hyena	813 lithics	Geraads 1995; Wood et al. 2013
76	Carihuela	VI	Spain	MP	MIS 3	1	Hyena	50 archaeological levels with plenty of Mousterian artefacts (but no Levallois production)	Carrión et al. 2019
77	Cova 120	Nivel IV-V	Spain	MP	MIS 3	2	Bear	198 lithics in total in levels IV (N = 140) and V (N = 58)	Agustí et al. 1991
78	Cova del Gegant	Galería GL-1, layers IIIa, XXIV and IV	Spain	MP	MIS 3	3	Hyena	ca. 60–100 lithics	

(continued on next page)

Table 3 (continued)

ID	Site name	Layer	Country	Period	Marine Isotope Stage	Site category	Focal carnivore context (hyena/bear)	Number of lithic artefacts	Reference(s)
79	Cueva de los Moros de Gabasa	a + c, d, e, f, g, h	Spain	MP	MIS 3	2	Hyena	ca. 4500 lithic artefacts recovered in all layers, ca. 25% retouched	Sanz et al. 2017; Daura and Sanz 2014 Utrilla and Montes 1986; Utrilla et al. 2010 Sala et al. 2020
80	Valle del Tejadilla site complex (Cueva del Búhu, Cueva de la Zarzamora, Portalon del Tejadillo)	CAM-1 & CAM-2(a, b)	Spain	MP	MIS 3	3	Hyena	16 lithics (Portalon del Tejadillo); Discoidal production with pseudo-Levallois points, cores, flakes and blades/bladelets	Sanchis et al. 2019
81	Llonin	Galeria (G): layer VI, Cono Posterior (CP): layer VIII	Spain	MP	MIS 3	2	Hyena	8 lithics; level VIII(CP): flake, sidescraper/convergent sidescraper, denticulate; level VI(G): flakes (Kombewa), end-/sidescrapers and a denticulate	Daura et al. 2017; Sanz et al. 2017
82	Cova del Coll Verdaguier	Unit 1, 2, 3	Spain	MP	MIS 3	3	Hyena	14 lithics in total from all three units (Unit 1–3), including pseudo-Levallois flakes	Rios-Garaizar et al. 2012
83	Labeko Koba	IX	Spain	Chatelperronian	MIS 3	3	Hyena	81 lithics including 1 broken Chatelperronian point; robust laminar technology	Villaluenga et al. 2012
84	Astigarragako Koba	Level III, IV and V	Spain	MP	MIS 3	2	Bear	Level III: a few Mousterian sidescraper and flakes; level V: >20 lithics, mainly flakes, notches, denticulates and some sidescraper fragments.	Rios-Garaizar et al. 2012
85	Ekain	X	Spain	Chatelperronian	MIS 3	3	Bear	11 lithics including two Chatelperronian points and mainly finished but broken tools	Jacobi et al. 2007
86	Bench Quarry	Bench Quarry “tunnel” (block with hyena dentary and blade point)	UK	LRJ	MIS 3	3	Hyena	1 blade point	Jacobi et al. 2007
87	Kent’s Cavern	“Cave Earth”	UK	MP/LRJ/UP	MIS 3	3	Hyena	Mixed assemblage: low lithic count including 9 blade points, 1 bifacial point, attributed to the LRJ; Late MP handaxes and scrapers; and UP artefacts (Aurignacian, Gravettian)	Jacobi et al. 2007
88	Soldier’s Hole	Natural Layer 4, artificial Spits 12 and 14	UK	LRJ	MIS 3	3	Hyena?	3 bifacial points	Jacobi et al. 2007
89	Hyaena Den		UK	MP/LRJ	MIS 3	3	Hyena	Low lithic count including 2 blade points and 54 probably MP artefacts	Jacobi et al. 2007; Jacobi and Hawkes 1993; Jacobi et al. 2006; Flas 2008; Wragg Sykes 2017
90	Badger Hole		UK	LRJ	MIS 3	3	Hyena?	17 LRJ lithics including 4 blade points, two possible blade point fragments and 11 blades from opposed platform cores plus other artefacts from different periods (Lower Paleolithic to Neolithic)	Jacobi et al. 2007
91	Pin Hole	“Lower Cave Earth”	UK	MP	MIS 3	3	Hyena		Jacobi et al. 2007; Currant

(continued on next page)

Table 3 (continued)

ID	Site name	Layer	Country	Period	Marine Isotope Stage	Site category	Focal carnivore context (hyena/bear)	Number of lithic artefacts	Reference(s)
92	Pin Hole	Pre-maxilla of a perinatal spotted hyena, associated with a leaf point imprint in a grey calcite-cemented block, East Passage	UK	LRJ	MIS 3	3	Hyena	MP artefacts including bifaces in a mixed assemblage 1 blade point	and Jacobi 2001; Jacobi et al. 2006; Flas 2008 Jacobi et al. 2007; Currant and Jacobi 2001; Jacobi et al. 2006; Flas 2008
93	Robin Hood Cave	Breccia and "Cave-earth", Western Chamber	UK	MP/LRJ	MIS 3	3	Hyena	10 blade points and 1 bifacial point of likely LRJ attribution; 94 MP lithic artefacts	Jacobi et al. 2007; Currant and Jacobi 2001; Flas 2008; Wragg Sykes 2017
94	Grange Farm	fine sand	UK	LRJ	MIS 3	3	Hyena	182 lithics, mostly broken and small flakes including blade points, notched flakes and a blade core	Flas 2008; Cooper et al. 2011
95	Coygan Cave	Upper layer	UK/Wales	MP	MIS 3	3	Hyena	5 lithics, including 3 later Middle Palaeolithic handaxes and 2 flakes	Pettitt and White 2012

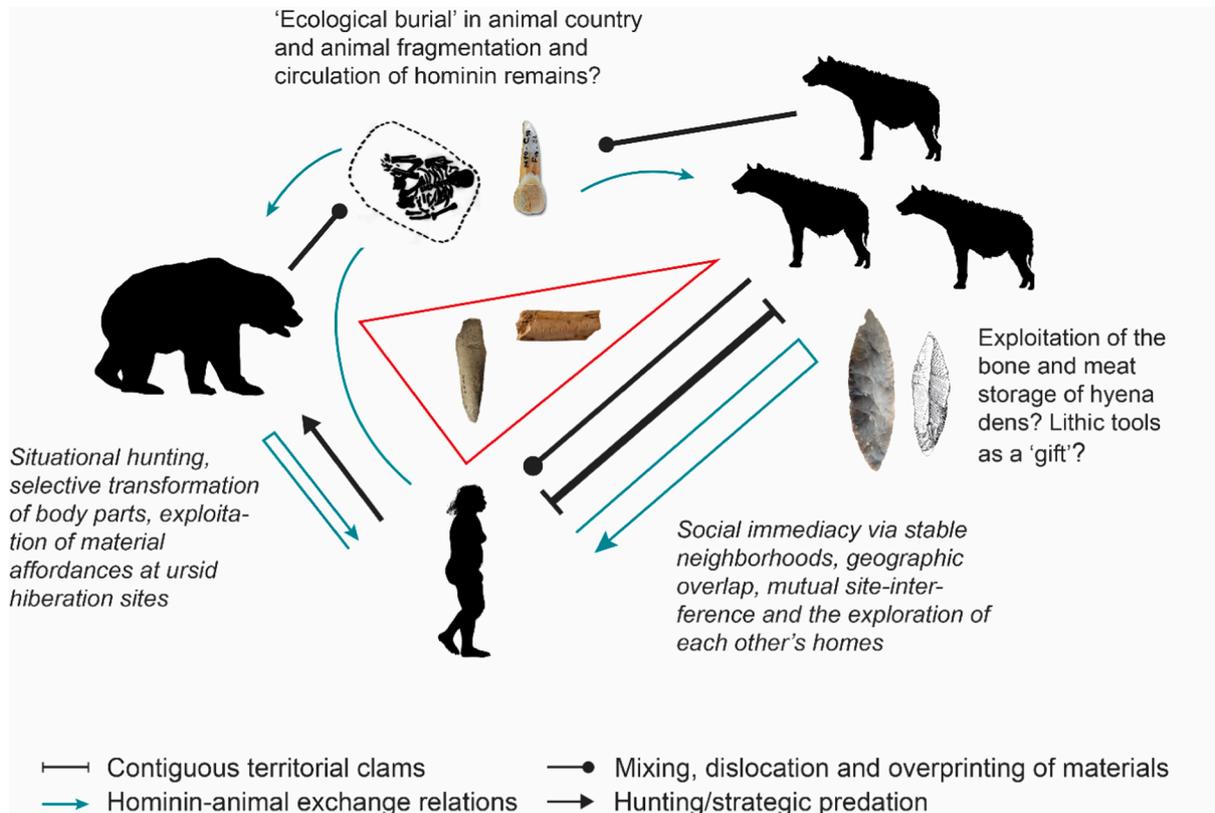


Fig. 3. Tanglegram of salient ecocultural relationships between hominins, hyenas and cave bears in the Late Pleistocene landscape. The red triangle denotes the latent field of multispecies sociality framing ongoing interspecies negotiations and 'emergent materialities' at the interface between hominins and hyena/bear others. Black outlines from <http://phylopic.org/> via the Public Domain; plan drawing of the Neanderthal burial from La Chapelle-aux-Saints reproduced from Tilley (2015: Fig. 9.1); photograph of a Neanderthal lateral incisor from the Quina Mousterian of Les Pradelles reproduced from Maureille et al. (2017: Fig. 4b); cave bear bone retoucher from Scladina reproduced from Abrams et al. (2014: Fig. 2); decorated hyena femur from Les Pradelles reproduced from d'Errico et al. (2018: Fig. 1); leafpoint from Ilsehöhle/Ranis (ID IV-1319) © M. Weiss/Burg Ranis and Jerzmanovice point from Zwergloch/Pottenstein reproduced from Richter (2009: Fig. 7). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hominin-hyena complementarity, home sharing and the lived significance of hyena-shaped locales. Former hyena occupations were inscribed into hominin site biographies and as such became phenomenologically *foundational* to hominin place-making. Hominin site selection in former hyena country, overlaying former hyena homes, may then *in itself* represent a strategy of relating and thus a means of promoting pluripresence with hyena neighbors. At sites like Teixoneres in Northeastern Spain, where detailed intraspatial analysis of Unit III has shown that Neanderthals respected the habitation area of hyenas – hominins occupying the areas close to the cave entrance and hyenas denning in the inner sheltered zones – and recurrently used the same sectors to house their short-term occupations (Zilio et al. 2021), it is certainly difficult to dismiss the layered multispecies history of the site as a place-defining feature. The structured palimpsest of these sites can be viewed as *framing* the phenomenology of place, rather than reducing palimpsest to a barrier of insight (cf., Bailey and Galanidou 2009), and hence testifies that Neanderthal landscapes also incorporated ‘the powerful fact that life must be lived amidst that which was made before’ (Meinig 1979: 44), both human and non-human.

Additional evidence for potentially meaningful ecocultural and material negotiations between hominins and hyenas comes from the LRJ (‘Lincombian-Ranisian-Jerzmanovician’; sensu Flas 2011) and related Late Middle Paleolithic/Initial Upper Paleolithic (IUP) techno-complexes in Northwestern and Central Europe (Bolus 2004a; Uthmeier 2004; Jacobi et al. 2007). At the classic type-locality of Ilsehöhle near Ranis in Thuringia, Germany (Hülle 1977), MIS 3 hominins left behind a small assemblage of finished Jerzmanovice blade points and symmetrical bifacial leaf-points in a cave bear and hyena-rich depositional context in close proximity to possibly penecontemporary hyena dens. The bifacial leaf points are particularly well-crafted and are made of high-quality Baltic flint, imported to the site from a distance of at least 30 km. These artefacts exhibit only limited traces of prior use or evidence for recycling and edge-maintenance as is otherwise characteristic for similar bifacial tools (cf., Iovita 2014; Weiss 2020). Fifteen of the 24 blade points and 13 of the 19 bifacial leaf-points were discarded in a complete, near-mint state (Hülle 1977: 106). The lack of any conclusive evidence for on-site toolkit maintenance opens up the interesting possibility that these certainly valued objects were deposited or at least abandoned in hyena country. This tentatizing reading provides an important challenge to standard subsistence-economic or simplicity-foregrounding interpretations of Late Middle Paleolithic/IUP hominin behavior rendering them as mere discard products, and, in line with the broader re-conceptualization of hominin-nature relations attempted here, thus re-configures the burden of proof as well as received assumptions on the hierarchy of evidence.

Other ‘type two’ and ‘type three’ assemblages from the Central European *Blattspitzengruppen* are similarly dominated by finished tools, especially partial and fully bifacial points, bifacial foliates and various bifacial knife-types (Richter 2009), and the operational sequences documented at these sites are frequently fragmented, with little or no evidence for initial stages of tool confection and primary blank production (Bolus 2004b; cf., Table 3). Furthermore, two notable examples for the recovery of a small number of finished tools in hyena contexts are provided by a single but typical Jerzmanovice point alongside a few plain flakes from Zwergloch cave (Müller-Beck 1968) and the exceptional Late Middle Paleolithic leaf points from Haldenstein (Riek 1938) in Southern Germany, both found in hyena-rich deposits. Another example is Kirchberghöhle near Schmädingen in Southeastern Germany, dated to between ca. 40 and 48 kya, where only four lithic artefacts, three classic Jerzmanovice blade points and a basal blade point fragment, plus a nondiagnostic fragment were recovered alongside a large faunal assemblage bearing a diagnostic hyena fingerprint (Uthmeier et al. 2018). Such potential practices of signifying hyena-invested places with non-local tools embodying hominin individual and group biographies may not only be understood as a symptom of hominin landscape socialization and enculturation, but coevally as a historically

situated attempt to negotiate the place of Neanderthals in hyena-saturated, carnivore-rich worlds.

A similar pattern of hominin-hyena coassociation has been noted for the LRJ in Great Britain (Jacobi et al. 2007; White and Pettitt 2011). Sites such as Kent’s Cavern, Hyena Den, Pin Hole and Robin Hood’s Cave all represent hyena-dominated archaeological deposits containing only a handful of finished lithic tools in mint or close-to-mint condition, again especially Jerzmanovice points and cognate pointed blade tools, as well as a few bifaces and bifacial points of likely slightly older Middle Palaeolithic origin (cf., Wragg Sykes 2017; Table 3), thus possibly similarly referencing the significance of these nonhuman places and the related deposition or placement of selected items of material culture as a form of relating, interspecies negotiation and meaning-making (cf., Fig. 3). At Coygan cave in South Wales, hyenas were the primary agents of accumulation while three Late Middle Palaeolithic handaxes and two flakes attest the short-term presence of Neanderthals at the site (Pettitt and White 2012: 336-337). The handaxes exhibit extended object biographies and are manufactured from non-local raw materials imported from sources ca. 20–40 km away. The curated artefacts were found in a peculiar position within the cave interior, turned against the north wall, and their deliberate caching has been considered (Pettitt and White 2012: 337) but remains difficult to securely establish given the poor documentation of the original excavations. Another special find illustrating possible depositional hominin behaviors in hyena territory comes from Bench Quarry ‘tunnel’ where a single leaf point on a blade was placed directly underneath a hyena jaw and taphonomic or post-depositional processes can be excluded as formative agents of this lithic-hyena association (Jacobi et al. 2007: esp. Figs. 54a-b).

At Grange Farm in Central England, radiocarbon dated to between 40 and 44 kya, a small assemblage of LRJ lithic artefacts including a complete and a broken leaf/blade point and a small number of trimming flakes related to on-site blade point maintenance were recovered next to an open-air hyena den and a few proposed meat storage pits for hyena cubs (Cooper et al. 2011). The articulation and intermixture of hominin and hyena signatures at Grange Farm is interpreted as evidence for MIS 3 hominins venturing into hyena territory (pace Pettitt and White 2012: 324), possibly to scavenge food caches in or close to hyena maternity dens (Cooper et al. 2011: 91). The archaeological data from Grange Farm (a ‘type three’ site) is thereby broadly consistent with a short-term ‘raiding party’ scenario involving only a few hominins, and generally supports the emerging complexity of hominin-hyena relations in MIS 3, including the interpretation of hyena spaces as an integral part of the broader ‘giving environment’ of Late Pleistocene hominins (sensu Bird-David 1990; see above). Drawing on Bird-David’s (1990: 190-191) anthropological insights, it might indeed be sensible to re-contextualize the broader observations from the Late Middle Palaeolithic and the LRJ in terms of an integrated system of giving and taking – and thus in light of generalized transspecies exchange theory (Nadasdy 2007) rooted in the social anthropology of the Maussian ‘gift’ (Mauss 1967; Peterson 1993).

As Nadasdy (2007) has pointed out, hunting-gathering lifeways – especially in northern latitudes and arguably independently of their specific hominin context – revolve around human-animal intimacy, co-dependency, mutuality and continuous *exchange*. Because of the existential significance of hunting and cognate practices in many small-scale Northern foraging communities, even seemingly inculpable, subsistence-oriented activities are fundamentally *social* and articulate the need to negotiate, maintain and reproduce human-world relations in which animal others regularly encountered or engaged are focal nodes. ‘Hunter-gatherer’, then, is not just an economic label, an adaptive signification or a ‘mode of production’ but instead denotes a general mode of being-in, relating to, and experiencing the world (Ingold 2000), with often varied but decisively non-Western ontological ramifications. Not only is there widespread recognition of the hunted animal as a ‘gift’ incurring future obligations and potential ‘counter-gifts’ on behalf of the hunter, animals are met as sociopolitical interlocutors, powerful as well

as potentially dangerous ‘trading partners’ and thus demand respect and reverence, often safeguarded by sophisticated cultural techniques (Nadasdy 2003: 83-108, 2007).

Ingold (2000: 61-76) argued that the relationship between the hunter and their prey is based on ‘trust’, in turn resting on bilateral autonomy and co-dependency. Indigenous people’s talk of animal others as ‘offerings’ or as ‘giving themselves’ to the hunting community – for example well-described in the context of circumpolar whale (Demuth 2019) or elk hunting (Willerslev 2007: 102) – is therefore not just ‘metaphorical’ or ‘symbolic’ as Nadasdy (2007) aptly reminds us, but instead expresses the lived social fact that animals are an integral part of society and as such participate in cycles of exchange and affirmation, just like other humans do, for example when they share meat or circulate objects to ascertain relatedness or belonging (i.e., as seen in the ‘Kula ring’ of Melanesia or potlach practices across North America; cf., Malinowski 1922; Nadasdy 2007: 28). Fuglested (2012: 18-21, 2018: Fig. 4.8) and others (cf., Corry 2011: 53f.) have framed the notion of the ‘hunting cycle’ to capture this reciprocal dynamic of giving and taking permeating the human-animal interface in many foraging societies. Importantly, however, and as already highlighted by Mauss (1967: 23), gifts are not always freely given and often require particular strategies to be facilitated. The implied reciprocity is also not always positive: reciprocal gift exchange may thus easily involve potentially adversarial relationships. What is more, the exchange relations themselves can be asymmetrical insofar as different ‘trading partners’ may give and receive gifts in different ways and by different means, and this makes social exchange particularly challenging to detect and examine in interspecies contexts.

Hominin depositional practices broadly construed – i.e., without necessarily involving structured or formal deposition – including assemblage mixing, object transformation and discard behaviors may then be reconsidered in the light of a broader logic of material and social exchange at the hominin-hyena interface. Taking from hyena places and hideouts, for example by scavenging and foraging bones and meat caches, may have implied the obligation to give something ‘hominin’ in return, and some of the finished and curated tools and the isolated pieces of human-modified bone encountered in hyena places may consequently be interpreted as evidence for situated and multi-stranded processes of interspecies negotiation and exchange. Material transformation and fragmentation may be regarded as a particularly potent locus of such generalized exchange relations since hyenas are the osteophagic raw material transformers and fragmentators *par excellence* and mimicking this behavior thus not only maps hominins onto hyenas, and in this way produces analogy, similarity and proximity, but perhaps also signifies the conviction to submit hominin materiality to hyena domains. Mixing itself may then be viewed as a community-creating practice. From this perspective, the image of the ‘raiding party’ invoked above is minimally misleading and reinforces resource-competition tropes rather than being attentive to the larger ecologies of exchange in which such practices are often embedded.

This integrated ecocultural framework also recognizes that abandoning hunting implements or stone tools more generally can hardly be considered a neutral act, as foraging people variously regard such objects as part of their ‘extended personhood’ (González-Ruibal et al. 2011; Walls 2019; Snow 2020) and/or maintain quasi-interpersonal relationships with them (Weedman Arthur 2018), again undermining received interpretive wisdom in Paleolithic archaeology based on long-standing nature-culture divisions. Given that proximate animal others are often regarded as ‘extended kin’ in such small-scale societies (cf., Norton-Smith 2010; Willerslev and Ulturgasheva 2012; Bird-David 2017a; Wisher and Kay 2020: 131), material exchange and mutual interference at the hominin-hyena interface have the capacity to promulgate lived multispecies communities transcending hominin-exclusive domains and behavioral registers and therefore potentially indicate non-analogue practices of transspecies ‘kin-making’.

Returning to the LRJ, another observation on MIS 3 hominin-hyena

entanglements is interesting. As noted by Discamps (2009), there is an interesting increase in hyena-bearing sites towards the end of MIS 3, both paleontological and archaeological, and different complementary lines of evidence point to a marked demographic expansion of Western European hyena populations in this timeframe – a ‘Hyena event’. Even though hyenas arrived in Britain already during the Eemian (Varela et al. 2010) and earlier (Turner 2009), the remarkable cluster of British LRJ sites, many of which yield ‘type three’ signatures and represent short-term occupations in or close to hyena dens with only a handful of lithic artefacts, mostly hunting implements and points (see Table 3), may be regarded as a reflection of LRJ hominins tracking hyena landscapes, and thus as indicative of the increasing abundance of hyenas in this area during the second part of MIS 3. Put more provocatively, irrespectively of whether Neanderthals or other Late Pleistocene hominins including potentially contemporaneous IUP *H. sapiens* groups were the bearers of this techno-complex (cf., Hajdinjak et al. 2021; Prüfer et al. 2021), the LRJ then possibly delineates the crystallization of long-term, high-mobility adaptations to hyena environments already prefigured in some Late Middle Paleolithic contexts. Re-formulated in multispecies terms, the LRJ may give testimony to a derived archaeological signature of being-with and becoming-with hyena others in the open and vast landscapes of Northern Europe. The LRJ may then circumscribe a mutually constructed niche – or a multispecies ‘meshwork’ to take up Ingold’s (2013) formulation – articulating large-scale sociomaterial consequences of Late Pleistocene hominin-hyena coordination and niche construction (see esp. Hussain and Will 2021 for the possibility of multispecies niche construction). At the very least, it is certainly worthwhile to reconsider the broad geographic correspondence between the larger LRJ phenomenon and the North European Plain which has likely acted as a major landscape attractor and mobility catalyst for Late Pleistocene hyenas.

As a final consideration, it is worth returning to the earlier mentioned circumstance that some Middle Paleolithic sites where both hominins and hyenas acted as formative agents (esp. ‘type two’ and ‘type three’ sites), especially in France, Italy and Spain (Diedrich 2014: Table 1), have also yielded isolated hominin teeth or other skeletal parts. Traditionally, it has been assumed that these hominin remains are intermingled with carnivore-derived deposits due to taphonomic processes, hominins falling prey to predators, for example as a result of ‘confrontational scavenging’ (Bunn and Kroll 1986; Baynes-Rock 2015b) or succumbing otherwise and then being transported to nonhuman occupation sites by various carnivores (cf., Camarós et al. 2016), and/or, finally, that the palimpsest character of the archaeological sediments makes it unlikely that the encountered hominin remains are contemporary with the activities of hyenas and other carnivores in the first place (e.g., Villa and Soressi 2000). Some hominin bones further exhibit carnivore modification marks and some even yield evidence for digestion by hyenas as seen at Les Pradelles (cf., Maureille et al. 2017), which is taken to lend support to the cited scenarios. All of these points are valid considerations but given the scarcity of formal, well-defined burial contexts in the European Middle Paleolithic (Pettitt 2011) and following the previous arguments for socioecological immediacy and a broader reciprocal ‘give-and-take’ logic underpinning Neanderthal-nature relations – above framed under the theoretical umbrella of generalized multispecies exchange relations (pace Nadasdy 2007) – other scenarios emanating from the situated sensitivities and animal-directed concerns of multispecies life should also be considered.

It is for instance possible that Neanderthals and other hominins engaged in what may sensibly be termed ‘ecological’ funerary practices, in which the deceased were offered to specific nonhuman co-inhabitants to be scavenged and ultimately recycled – broadly analogous to Tibetan sky burials and related cultural practices already described by anthropologists (Martin 1996). It should be noted that Neanderthal ‘funerary caching’ (Mussi 1988: 99; Pettitt 2011: 92) is not inconsistent with this scenario (cf., Pettitt 2018), especially if we accept hyenas as important agents of hominin landscape enculturation, and given that the animals’

ecosystem role is tied to recycling key nutrients in bones (Abraham et al. 2021) and, generally speaking, transforming bodies – i.e., their agency is phenomenologically linked to the transposition of corpses and takes part in the wider ecological *chaîne opératoire* of bodily forms, thus fundamentally regulating and curating Middle Paleolithic ‘bodiescapes’. Isolated hominin remains at carnivore sites may accordingly attest to the deliberate fragmentation of hominin bodies linked to the deposition of some body parts, as discussed in the context of Les Pradelles and similar to the meaningful placement of stone artefacts considered above, at liminal places in the landscape where the relationship between human and nonhuman was at stake and negotiative action was required. And, lastly, some of these scattered remains may simply give testimony to the hazardous nature of venturing into the territories and homes of carnivores, yet not merely as deprived evidence for a ‘nasty, brutish and short’ life (pace Hobbes) but as part of ongoing efforts to relate to and address significant nonhuman co-inhabitants.

### 3.3. Bears: Slumbering companions walking between worlds

The so far developed perspectives on the significance of carnivore others, especially hyenas, can be complemented by a brief foray into Neanderthal relationships with bears. Cave bear remains are frequently encountered at Neanderthal sites across Eurasia – even though many instances are interpreted as alternating, non-related occupations (Patou 1988; Stiner 1999) – and they co-occur with hyena assemblages in many important ‘type two’ and ‘type three’ sites (Hoffecker and Cleghorn

2000; Viranta and Grandal d’Anglade 2012; Skinner 2012). Interestingly, there is a marked east-southwest gradient, with cave bears being more dominant and consistently entangled with Middle Paleolithic sites in Central, East-Central and Southeastern Europe (cf., Daujeard et al. 2016; Romandini et al. 2018: Fig. 1), while hyenas seem to have been the primary spelaeoid interlocutors for hominins in Western and probably Southwestern Europe (cf., Jimenez et al. 2021; Fig. 4; see Table 3). This geographic division is probably linked to the characteristic heterogeneous relief of East-Central Europe and the circumstance that many of these areas retained a noteworthy forest or forest-steppe component and even acted as cryptic refugia for various tree species during glacial conditions, especially below 45°N and for example in the Balkans (Birks and Willis, 2008; Tzedakis et al. 2013; Ravnsbæk Holm and Svenning 2014). The boreal refugia and mountainous environments of Southern Europe, notably Italy and Austria, probably played a similarly conducive role for hominin-bear encounters and interactions.

This division between Western and Central/Eastern Europe coincides with bear palaeogeography: in Western Europe, Neanderthals mainly had to deal with the common cave bear, *U. spelaeus*, whereas Central European and Eastern Neanderthals shared their environment with the largest and most powerful Late Pleistocene bears, *U. ingressus* and *U. arctos* ‘priscus’ (cf., Baca et al. 2014; Marciszak et al. 2019; Marciszak and Lipecki 2020: Fig. 2). This not only suggests divergent conditions of interaction and modes of lifeworld intersection but also raises the interesting possibility that geographically distinct bear assemblages co-evolved with different Neanderthal subpopulations reflected in genetic

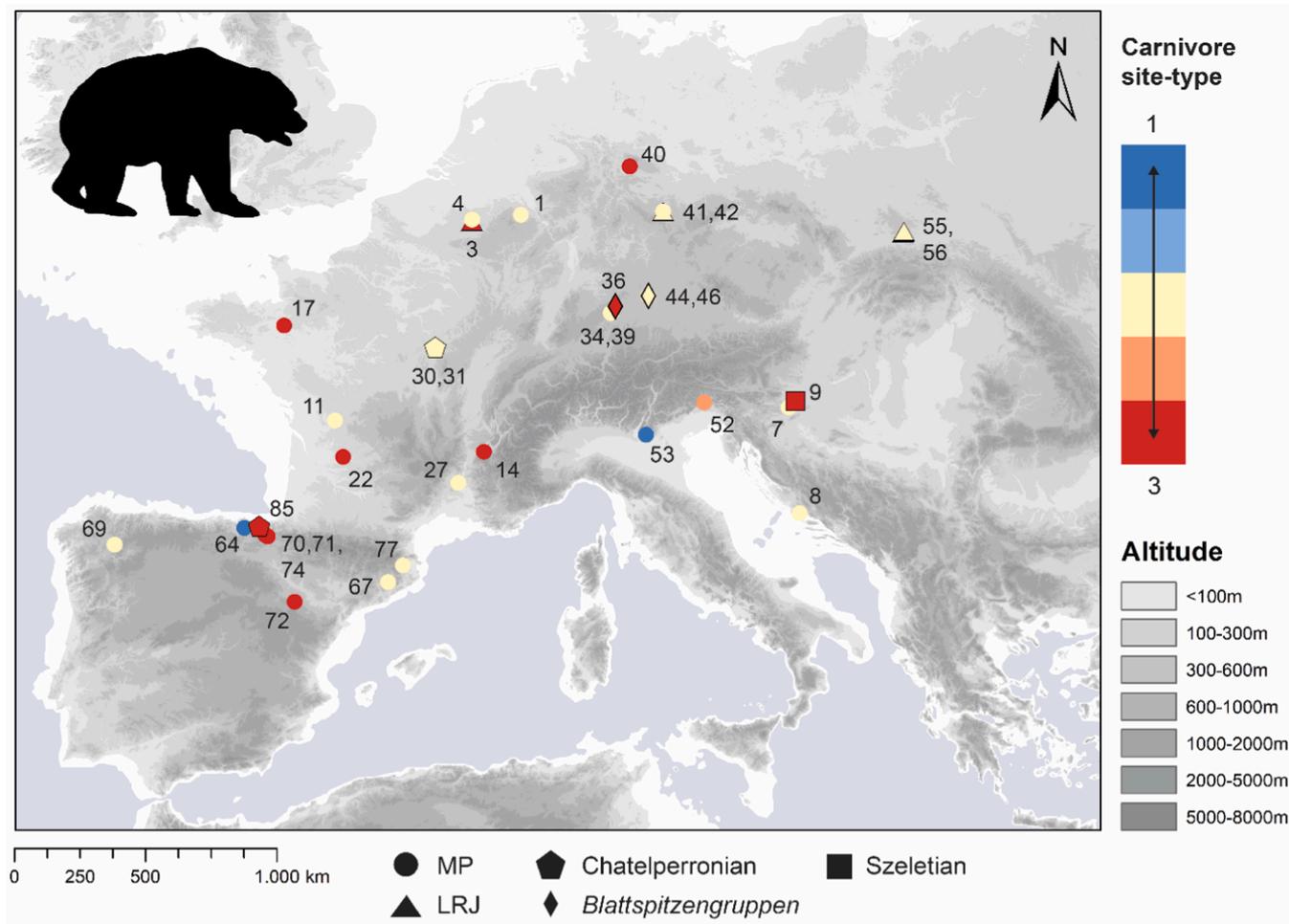


Fig. 4. Middle and incipient Upper Paleolithic sites with significant bear input mentioned in the text and/or listed in Table 3 (site numbers correspond to site IDs in Table 3; Zaskalnaya VI and Matuzka are located outside of the shown map section). Colors indicate inferred site category and shape of symbols represent period/ techno-complex contexts (MP = Middle Paleolithic; LRJ = Lincombian-Ranisian-Jerzmanovician). Animal outlines from <http://phylopic.org/> via the Public Domain.

(Dalén et al. 2012; but see Hajdinjak et al. 2018) and lithic technological data (Ruebens 2013). Such structured cogeographies have been demonstrated for contemporary First Nation groups and grizzly bears in Western Canada (Henson et al. 2021), indicating that foragers and bears often have aligned needs in terms of space, food and other resources and are thus drawn to the same habitats, so that bears easily emerge as cardinal nodes in integrated human socio-ecological systems.

In contrast to hyenas who tend to be gregarious, inquisitive and resource-competitive, cave bears are unlikely to have assumed a role as tangible and physically contiguous, 'apresent' neighbors (sensu Schütz 1993) and encounters between bears and hominins were likely framed by specific situations and bound to particular locales. As shown by occasional evidence of Middle Paleolithic encounter hunting (e.g., Münzel and Conard 2004) cave bears and Late Pleistocene hominins were drawn together in karstic environments (Daujeard et al. 2016) and potentially interfered with one another while seeking shelter and, in the case of spelaeoid bears, places for hibernation. Based on archaeozoological evidence from Balve cave, Kindler (2012) has suggested that Neanderthals must have developed a habit for scouting and perhaps even clearing caves before establishing their own occupations. But Neanderthals also visited cave bear retreats independently of occupational concerns, sometimes in remote places such as high-up in the Alps (Richter 2018), and bequeathed isolated hominin cut-marks on bear bones (e.g., Martínez-Sánchez et al. 2012). In addition, earlier interglacial Neanderthals recurrently, and sometimes systematically, 'harvested' cave bears close to hibernation sites, in wetland settings and/or at prominent river confluences, and took their fur and perhaps meat in addition to high-value consumables such as the tongue (Wragg Sykes 2020: 158). This targeted hunting pattern is for example documented at Taubach in Germany (Bratlund 1999), Biache-Saint-Vaast in France (Auguste 1992) and Krapina in Croatia (Miracle 2007) and aligns with ungulate predation tactics discussed before.

In Taubach, bear skulls are particularly numerous and Neanderthals also took special interest in the paws of the animals (Bratlund 1999). In contrast to what might be expected, *U. arctos* bones yielded most cut-marks at Biache and Taubach (Auguste 1992; Bratlund 1999; cf., Romandini et al. 2018: 87) and this suggests that Neanderthals to a lesser extent took advantage of the marked 'homing behavior' and den fidelity of spelaeoid bears but instead preferred to intercept large carnivorous brown bears in opportunistic foraging situations or when attempting to hibernate close to cave entrances (and *not* deep inside cave bodies; cf., Marciszak and Lipecki 2020: 888). This is consistent with Auguste's (1995) observations regarding the Biache material, where cubs are generally missing and the age and sex distribution of killed bears supports an interception scenario of solitary individuals, rather than hominin stalking of hibernating ursids in underground cavities. The clear processing focus on cranial bones and especially mandibles, jaws and paws derived from prime-aged bears (cf., Bratlund 1999: 118) seems hardly coincidental then, and supports the view that Neanderthals were also being concerned with 'harnessing' specific behavioral and foraging qualities linked to these body parts, which clearly define brown bears as foragers. This possibly indicates a general concept of character transposition and trait fluidity at the Neanderthal-animal interface, which is well-documented among contemporary and historic hunter-gatherer societies and frequently provides a fundamental ontological rationale for the selection, transformation and utilization of specific zoomaterials (Hill 2012, 2019; Qu 2017).

This pattern of targeted bear exploitation with an emphasis on MIS 5 contrasts with Neanderthal-ursid engagements in later Middle Paleolithic contexts, especially in the Italian Alps of MIS 3, where hominins seem to have conducted foraging trips to mountainous and sometimes high-altitude bear denning locales and indiscriminately processed hibernating spelaeoid bears of all age classes during winter and spring (Romandini et al. 2018; Wragg Sykes 2020: 158). These alpine contexts, comprising sites like Fumane, Rio Secco, Generosa Cave and Cio Ciara, document a more integrated foraging strategy where rugged terrain prey

such as ibex and deer complement opportunistic but nonetheless intense bear exploitation of entire carcasses including the fatty chest, limb parts and also bone marrow extraction, with occasional evidence for the transport of high-value meat-bearing parts between sites (Wragg Sykes 2020: 157-158). The responsible Neanderthals thus clearly took advantage of the seasonal schedule and rhythm of characteristic cave bear 'homing behavior' (Marciszak and Lipecki 2020: 888), rendering ursids a seasonally predictable resource.

Yet bear hideouts and hibernation dens in or at the edge of mountainous landscapes were not only foraging grounds in the Late Middle Paleolithic, they also framed multispecies 'contact zones' with their own distinct material affordances and possibilities. They offered rich, natural bone caches with a raw material potential of their own, and hominins sometimes manipulated and dislocated skeletal material from these bear-derived bone beds (Romandini et al. 2018). The recently discovered cave bear bone retouchers from Scladina (Abrams et al. 2014), Rio Secco (Romandini et al. 2018) and Fumane (Jéquier et al. 2012) may be regarded as 'emergent materialities' of this larger interspecies constellation, in which hominin-bear relationships were negotiated at specific localities and situations in a wider 'hunter's landscape' (pace Ogdén 2011; Fig. 3). The sequentially incised cave bear bone recovered from the hyena and cave bear-dominated sediments of Pešturina cave in modern-day Serbia can similarly be interpreted as such situational material engagement linked to special bear-endowed places in the wider landscape (Majkić et al. 2018). In the Northern Caucasus, the role of cave bear-invested places may even be reflected in the intermediate or 'transitory' position of sites such as Matuzka in larger Neanderthal land-use systems, occupying a key nodal position between lower and higher elevations (Hoffecker and Cleghorn 2000). Matuzka has yielded only a small number of Middle Paleolithic stone artefacts within otherwise cave bear-dominated sediments and its archaeology is most parsimoniously interpreted as a reflection of multiple recurrent but short-term hominin stays (Hoffecker and Cleghorn 2000: 372, Fig. 2). Some bear localities at the periphery of Neanderthal core territories thus likely developed into ephemeral but persistent places (pace Maher 2021) or integral waypoints in seasonally differentiated cultural landscapes of the terminal Middle Paleolithic. After all, landscape is always, as Crumley (1994) has pointed out, 'an array of lived experiences made manifest' (Maher 2021: 249) where hominin interference with space and its inhabitants contributes to the making of 'place'.

The importance of ursid places in Neanderthal landscapes may also be gleaned from Middle Paleolithic burial practices. As outlined by Camarós et al. (2017), the Neanderthal burial of La Chapelle-aux-Saint in Southwestern France may provide tentative evidence for the utilization of *refurbished* cave bear hibernation pits. The heated controversy on the intentional character of Neanderthal burials (Rendu et al. 2014, 2016; Dibble et al. 2015) may then, in some instances at least, beg the actual question at hand and only detract attention from the 'hybrid' quality of the burials as partly anthropogenic and partly zoogenic. Following Hill (2000), such interments can be regarded as vibrant 'microcosms' of lived human-animal relations, and they powerfully counter received Western bifurcations of 'nature' and 'culture' (or the supposed cognitive and cultural implications of formal vs. informal burials). As Pettitt (2015) has already noted, Neanderthal-type interments are hardly intelligible as proper 'ritual burials', but instead appear to signal a set of cultural practices for which the *fabrication and affirmation of proximity* to the surrounding land was imperative. Such 'ecological' funerary behavior embedded in multispecies geographies and tied to specific more-than-human places must be examined as *born out* of the conditions and dynamics of multispecies encounter and interaction rather than merely signposting their aftereffects. Material fragmentation and the disarticulation of bodies was an integral part of these Neanderthal practices of relating and they may be understood, as proposed above, as part of broader efforts to negotiate familiarity and intimacy via *mimicry* and *re-enactment* – communicative modalities that often play a key role in how contemporary hunter-gatherers address a range of key

actors in their environments including other animal species (e.g., Lewis 2014). Although the co-optation of bear-dug structures by Middle Paleolithic hominins remains somewhat speculative until more supportive evidence is recovered, bear places themselves also frame some Neanderthal interments. At Regourdou, for example, a Neanderthal burial is associated with a natural, albeit catastrophic denning profile of brown bears and three cut-marked bear bones indicate at best sporadic hominin visits to an otherwise bear-vested locale (Cavanhié 2011), thus encouraging the interpretation that the placement of the deceased into bear country was not fortuitous.

#### 4. A new narrative?

Multispecies theory sets the stage for new narratives and alternative understandings of early human evolution and the making of our species. Patterns and trajectories of hominin becoming are often the product of mutual and ongoing co-shapings of humans and nonhumans, and animal others have played a key but understudied role in this process. We have tried to argue here that much of the archaeological evidence traditionally deployed to reconstruct hominin subsistence behavior or the symbolic and cognitive capacities of hominins in fact presents a rich corpus for rethinking interspecies relationships in deep prehistory. The resulting redressing of hominin-animal interactions, through the prism of integrative multispecies theory and interdisciplinary anthrozoology, draws attention to the reciprocal interweaving of hominin and animal behaviors and the productivity of the emerging, often co-adaptive interfaces in modulating behavioral constraints and opportunities, broader land-use and mobility patterns, and signatures of material culture. Other-than-*H. sapiens* material culture which references animals, such as deliberately modified and decorated animal bones or extracted and then co-opted animal body parts such as claws, feathers and limb bones, thereby actively takes part in the construction and continuous negotiation of interspecies relations. These instances of material culture, rather than indexing abstract symbolic or cognitive *deus-ex-machina* qualities, are consequently *imbricated* in the very hominin-animal interactions they shape, affirm and reproduce – they do not stand ‘outside’ of or transcend these relationships and their study is thus essential.

Making and handling material culture is a *mode of relating in itself*, and the archaeological challenge is to reinsert different material expressions of the archaeological past back into their multispecies ‘meshworks’ (sensu Ingold 2013). Deliberately incised bones of corvids, hyenas and giant deer (Leder et al. 2021) or the suspended or otherwise worn eagle and owl talons of Eurasian Neanderthals then first and foremost attest to the socioecological and phenomenological significance of concrete lifeworld intersections between the involved hominins and the addressed animal others. There is no need to account for this material culture in terms of a *priori* biocognitive determinisms, prioritizing inbuilt capacities, extended phenotypes or fossil minds. To the contrary, such animal-imbued material culture can be understood and contextualized by taking stock of the tangling of behavior and lived experience at prehistorically situated hominin-animal interfaces, precarious or not, and by recognizing that different types of interspecies neighborhoods and modes of landscape sharing can modulate particular ‘horizons of concern’ and sociomaterial practices on both sides. These social practices of course have cognitive and aesthetic extensions, but not the other way around.

This reframing of hominin-animal relationships not only suggests that animals such as raptors, hyenas and bears actively shaped, and thus co-defined, the lifeways and material cultures of Neanderthals and other Late Pleistocene hominins, it also, and perhaps more importantly, deconstructs received dualist evolutionary narratives, which too often divide the human story into an earlier, ancestral stage ‘poor’ in culture and mind and a later, derived stage ‘rich’ in both of them. The here-presented multispecies exploration, conversely, suggests that the Neanderthal world was deeply, and probably from the beginning, impregnated with culture, expansive sociality and mind, and

interspecies relations were an important locus for all of them. Nevertheless, Neanderthals probably lived in differently constituted ‘nature-cultures’ when compared to later Upper Paleolithic *H. sapiens*, and hominin modes of engaging, living and becoming-with other animals were generally subjected to substantial evolutionary and contingent historical change. The various issues and questions raised by at least a decade of heated paleoanthropological research and debate on behavioral modernity and complexity and their many extensions and side-discussions – even though having certainly passed their heyday now – have thus unfortunately resulted in a misplaced concern with ‘origins’, rather than fostering the development of a comparative and deeply contextual approach to the shifting variables of hominin culture and society, including its anchoring interspecies nexus. What it means to be a Neanderthal in different times and places can only be answered by integrated ecocultural approaches confronting hominin and nonhuman realities, productions and concerns, and such analysis needs to make space for non-analogue variation in cultural behavior and interspecies dynamics to avoid the pitfalls of sapienscentrism. Responding to Sli-mak’s (2019) timely call for a ‘cultural anthropology’ and serious comparative ‘ethology’ of Neanderthals therefore requires to develop new contextual approaches that belabor the multispecies conditions of Neanderthal life, culture and materiality.

This lurking synthesis of ‘ethnographic’ and ‘ethological’ aspirations in Neanderthal archaeology – in sync with Lestel’s (2006) call to arms in animal studies – requires taking on the broad picture, and to also rechart hominin-herbivore interfaces in more-than-economic terms. A privileged starting point would be Neanderthal-elephant relations since elephants were, except for a few cases, probably opportunistically taken and scavenged (Uthmeier 2006; Smith 2015), yet their skulls were nonetheless transported to Neanderthal sites, and in Spy perhaps used to structure hominin space (Wragg Sykes 2020: 146–147), while elephant ribs were sometimes transformed into hammock-like pointed tools or points (Gaudzinski et al. 2005). The role of reindeer in the Quina Mousterian, briefly mentioned above, is another obvious locus of multispecies investigation in the Middle Paleolithic and might shed new light on the extent and nature of Neanderthal reindeer adaptations. More generally, it is striking how particular bones of selected animal taxa were used and transformed in particular ways (Wragg Sykes 2020) and this implicit normativity of raw material selection and transformation – for example the strong entanglement of bovid bones with *lissoirs* (Martisius et al. 2020) or the link between cervid femora and organic retouchers (Jéquier et al. 2015; Castel et al. 2017; Costamagno et al. 2018b) – is certainly indicative of lived concerns and interspecies relations embedded with meaning. These cases illustrate that not only carnivores but other animals as well co-structured the behavior and material culture of European Neanderthals, and that these hominins, in turn, maintained intimate, phenomenologically-informed and culturally consequential relationships with a broad range of nonhuman others. This not only demonstrates that Neanderthals lived in a vibrant ecology of relations but warrants further anthropologically-inspired investigations into the motivations and ontological ramifications of co-opting particular animal parts as tools and ornaments, and not others (see Hussain and Breyer 2017; Hill 2019; see above).

The Late Pleistocene is arguably a privileged arena for investigating the material consequences of multispecies relationships because ecological and faunal communities experienced severe continual reorganizations and the archaeological record documents major changes in hominin lifeways and culture from Western Eurasia to Southeast Asia and into Sahul (Roebroeks and Soressi 2016), most notably the emergence of representational imagery, which in Europe and Oceania centers on animal motifs (Bourrillon and White 2015; Brumm et al. 2021). An explicit multispecies framing of hominin-animal interstices in the Late Pleistocene helps to throw these consequential developments into novel perspective. Faunal and taphonomic evidence from the site of Les Cottés in Western France covering the Middle-to-Upper Paleolithic transition has been interpreted as indicating changing expositions between

hominins and carnivores through time – from ‘shared access’ to sites and bones in the Middle Paleolithic to the increasing ‘exclusion’ of other carnivores from hominin occupations and their ultimate demise during the Early Upper Paleolithic (Rendu et al. 2019). Similar trajectories of hominin-carnivore dynamics have been reported from other key stratigraphies in Central and Western Europe (e.g., Castaños 2005; Davis et al. 2007; Arsuaga et al. 2011; Enloe 2012; Conard et al. 2012; Kitagawa et al. 2012; Kitagawa 2014; Bertacchi et al. 2021). The periods following the Middle-to-Upper Paleolithic transition in Central and Western Europe are also associated with an increasing grasp of hominins on their surrounding landscape, resulting in more extensive settlements and a growing anthropogenic fingerprint (Baumann et al. 2020; Bocherens 2018), indicating changing modes and logics of hominin landscaping, place-making and ecosystem impact (cf., Anderson et al. 2018).

The Middle-to-Upper Paleolithic transition additionally marks a tipping point with regard to the systematic exploitation of animal carcasses anchored in the transformation or co-optation of nearly all animal body parts and animal-furnished raw materials, including previously less utilized materials such as teeth, antlers and ivory – a development described by Richter (2018: 202) as preempting a momentous ‘bone technique revolution’ in later MIS 3. This development may imply, or lay the foundations of, a fundamental rupture with obligatory and facultative scavengers co-inhabiting the landscape with Paleolithic hominins, and thus might have changed the role and significance of hominins as carcass accumulators for these other animals, perhaps most notably for bone-cracking hyaenids. Later hominins, most likely *H. sapiens* populations, laid claim to the totality of hunting yields and in this way substantially reduced the sense of co-ownership and sharing with other carnivores, possibly even promoting ‘amensalism’ (negative association). Given the strong emphasis on Neanderthal-carnivore competition and antagonism in the expert literature, it is somewhat ironic that it might have been this essentially post-Middle Paleolithic development largely tied to *H. sapiens* practices that possibly tipped the scales towards acute resource antagonism, and hence subverting the fragile but sympatric hominin-carnivore intersections that have evolved over thousands of years. If incipient *H. sapiens*-constructed cultural niches comprised domestic dogs, as recently proposed by Shipman (2015a, 2015b), this would have introduced yet another distance-promoting and ‘horizon of concern’-shifting element with potentially cascading effects for hominin-carnivore ecosystem expositions.

Another long-term trajectory in the evolution of hominin lifestyles and nature relations is associated with the Late Pleistocene drawing to a close: while archaeological evidence for ‘delayed-return’ foraging economies (sensu Woodburn 1980, 1982) remains largely absent from the Middle Paleolithic record, some Upper Paleolithic societies document the development of food storage practices (Soffer 1985; Soffer et al. 1996; Soulier and Costamagno 2018), anticipatory lithic blank caching or even ‘hoarding’ (Angevin and Langlais 2009), the expansive labor-intensive investment into delayed-return technologies including organic tools with extended life history (Liolios 2006; Bon 2015) and perhaps socially-controlled access to space, resources, knowledge and skill (Pelegrin 2013; Julien and Karlin 2014; Langlais 2020). Although these landmark developments seem to be staggered in time and do not emerge as a single coherent package, they nonetheless signal a time-transgressive, albeit not necessarily irreversible, departure from strict ‘immediate-return’ systems of ecocultural organization (pace Woodburn 1980; cf. Testart 2012) which have characterized much of the European Middle Paleolithic. This shift may be epochal as Bird-David (2006) has developed a range of convincing arguments suggesting that especially delayed-return foragers, for example the many contemporary Indigenous societies of the circumpolar North (Morphy 1999; Plumet 2006), are prone to develop and invest into elaborate animal-depicting visual culture, while their present-day immediate-return counterparts tend to exhibit reduced interest in such representational imagery.

This relationship does not reference some mysterious

anthropological universal, however, but rather appears to be a result of the specific interplay of economy and sociality in these communities and the proximity-dissolving consequences of delayed-return foraging systems, in which immediacy and co-presence are not regulative ideas or world-making principles anymore. In elaborate art traditions which are in many cases also characterized by the sophisticated decorative practices – representational and non-representational – with regard to everyday objects, the visualization of ‘others’ including animals serves in part as a means to engage, evoke or address these others and to *produce* immediacy, adjacency and social proximity in the first place (Bird-David 2006). A key function of material culture bearing figurative images, then, is often to re-enact the agency of the depicted beings in order to foster pluripresence and communication. For immediate-return foragers, by contrast, there is often no acute need to invest in such social technologies or cultural techniques that establish copresence with their communities of significant nonhuman others because pluripresence is safeguarded and continuously reproduced by their very way of living.

Against this broader background of human-nature relations and their cultural consequences, we propose that some carnivores – especially hyenas, raptors and bears – need to be considered socially significant others for Late Pleistocene hominins, and Neanderthals in particular seem to have invested material and cultural resources into forging reciprocal ties with these animals. We suggest that this is not just indicative of the ecological status of Neanderthals in the larger carnivore guilds of their time, but points to the phenomenological and society-permeating significance of animals with whom they shared, and regularly intersected in, the landscape. Being a carnivore and relating to carnivore others was likely a cultural concern for Neanderthals, and the biocultural evolution of these hominins must thus probably be understood in relation to broader patterns of evolving carnivore ecologies. The ecocultural entanglement of Neanderthals, hyenas and raptors across the vast expanses of the Eurasian mammoth steppes can therefore arguably be recognized – echoing Stewart’s (2005, 2007) seminal ecological arguments cited in the beginning of this paper – as a co-adapted community of on-par carnivore neighbors and interlocutors, stabilized by particular material and sociocultural practices of engagement, attunement, recognition and affirmation. In this view, the demise of Late Pleistocene scavenger-rich ecological communities in which Neanderthals actively participated is perhaps not only a byproduct of global dynamics of Late Quaternary megafaunal extinctions, but was possibly also fueled and accelerated by the emergence of cultural behaviors violating the balance of sharing and disrupting a sensitive matrix of co-adapted and carefully coordinated behaviors at the dawn of the Upper Paleolithic – undermining a broader Middle Paleolithic carnivore ‘commons’ (pace Baynes-Rock 2013).

Interestingly – and even though the archaeological and palaeogenetic evidence on the likely hominin bearers of the Northwestern and Central European LRJ is likely to tip in favor of early *H. sapiens* populations rather than late Neanderthals (or show that both demes contributed to its formation) – the LRJ and other ‘transitional’ or ‘Initial’ Upper Paleolithic complexes such as the Bachokirian (Hublin et al. 2020), the Bohunician (Svoboda 2003; Valoch 2013b) and possibly the Western European Châtelperronian (Rios-Garaizar et al. 2012; Discamps et al. 2019) seem to showcase a typical Middle Paleolithic signature when carnivore faunal fingerprints, site formation histories and relationships are concerned. This in turn may suggest that the significance of carnivores for Paleolithic societies was not primarily a question of hominin taxonomy and hominin-carnivore correlations, and that the latter were possibly continuous across the Middle Paleolithic-IUP transition. Yet, the reorganization of hominin societies precipitated by the developments between ca. 60 and 40 kya and eventually leading to the fully developed Upper Paleolithic still marks a turning point in the deep prehistory of Western Eurasia. Not only in terms of long-term material culture trajectories but equally so in the evolution of hominin-carnivore interactions – and thus likely heralding shifting regime dynamics of ecosystem assembly and hominin as well as carnivore roles therein,

linked to both changing ecoclimatic conditions and hominin technological and sociocultural practices.

The discovery of ‘recent Neanderthal ancestry’ in incipient *H. sapiens* populations associated with the IUP from Bacho Kiro (Hajdinjak et al. 2021) certainly adds to this emerging picture of a complex mosaic of continuity and rupture at the Middle-to-Upper Paleolithic juncture, and, instead of reassuring untenable Neanderthal-*H. sapiens* polarities, points to overlapping lifeworlds and cultural logics supporting similar carnivore relationships – a contestation perhaps indirectly supported by the emerging aDNA picture, according to which Europe between 45 and 40 kya was populated by more-or-less Neanderthal-like populations rather than genetically distinct Neanderthal and *H. sapiens* subpopulations (Fu et al. 2014, 2015; Prüfer et al. 2021). The pierced bear teeth recovered from the IUP layers of Bacho Kiro cave (Hublin et al. 2020) at least seems to continue a trajectory of intensification, and perhaps diversification, in hominin-bear relationships already prefigured in the later Middle Paleolithic.

## 5. Conclusions

This paper has taken some initial steps to unravel the ‘humanimal’ dynamics and conditions of later hominin evolution (pace Haraway 2007) beyond the confines of *H. sapiens* prehistory. We have shown that the deep-time evidence harnessed by Paleolithic archaeologists is by no means mute about the involvement of other animals in the making of hominin cultures and livelihoods, and suggests that perhaps especially carnivores have played a salient role in long-term human-nature negotiations among Neanderthals and other Late Pleistocene hominins with elevated carnivory. We have drawn on macroarchaeological evidence on the patterned associations and intersections of MIS 5–3 hominins and carnivore others in Western Eurasia to argue that engaging and addressing nonhuman carnivore others, especially hyenas but also large raptors and some bears, was an important dimension of cultural niche construction and world-making among pre-Upper Paleolithic societies, underscoring the lived significance of finding a place in the larger carnivore community. Carnivores thus actively participated in Neanderthal societies and relating to them was a fundamental sociological, and thus more-than-economic concern. The redressing of hominin-carnivore interaction attempted here therefore suggests that sympatry was likely a foundational pillar of Neanderthal-carnivore interaction.

Contrary to common views and previous interpretations in (Middle) Paleolithic archaeology, we have proposed that the competitive exclusion of other carnivores and their increasing detachment from hominin’s immediate ‘horizons of concern’ was bound to a fundamental regime shift in hominin-carnivore relations at the passage from the terminal Middle Paleolithic to the developed Upper Paleolithic. We raise the possibility that a new set of hominin cultural behaviors, in particular the aspiration to claim total prey carcasses for supporting a diverse portfolio of organic tools and visual cultures, eventually undermined co-evolved socially and materially productive ties with other carnivores and thereby foreshadowed the ultimate extinction of some species, notably obligatory scavengers adapted to hominin carrion landscapes, in the course of the Pleistocene. Our multispecies exploration further suggests that the development of animal-themed visual culture and figurative art in the Upper Paleolithic may have less to do with so-called ‘modern human behavior’ than with the conditions and situated logics of human-animal relationships and the (changing) role and contribution of nonhuman animals to hominin life, material culture and society.

Taken together, this paper cautions against the image of the ecologically ‘authentic’ carnivore, as other carnivores have lived in close neighborhood to hominins for over 3 to 4 million years and thus had plenty of opportunity to adapt to various hominin-shaped and inhabited landscapes. Hominins alike are too easily dismissed (or overlooked) as past ecosystem agents, even though their cultural practices and behavioral proclivities can profoundly modulate ecosystem dynamics. Hominins and carnivores have shaped each other for thousands of years and

the resulting behaviors, adaptations and dispositions must be considered a shared yet contested evolutionary legacy. Reconsidering Neanderthals and other hominins in the light of multispecies theory may unlock and clarify some of these legacies and opens up new windows into socio-cultural coordinates of Pleistocene life.

## CRedit authorship contribution statement

**Shumon T. Hussain:** Conceptualization, Data curation, Investigation, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Marcel Weiss:** Data curation, Investigation, Writing – review & editing. **Trine Kellberg Nielsen:** Data curation, Investigation, Writing – review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

This paper has a history of co-becoming of its own. We wish to express our gratitude to our students, who, through their enthusiasm and inspiration, have contributed to the completion of this paper. We thank our home institutions and affiliate research groups for providing intellectually stimulating and safeguarded environments. This paper is dedicated to the recognition of our multispecies past and its many legacies as well as the contemporary conservation of hyenas, raptors and bears.

## Funding information

STH acknowledges funding through the CLIOARCH project supported by the European Research Council under the Horizon 2020 programme (grant agreement No. 817564). TKN received funding from the Independent Research Fund Denmark (case number 9062-00027B).

## References

- Abay, G.Y., Bauer, H., Gebrihiwot, K., Deckers, J., 2011. Peri-urban spotted hyena (*Crocuta crocuta*) in Northern Ethiopia: diet, economic impact, and abundance. *Eur. J. Wildl. Res.* 57, 759–765.
- Abraham, A.J., Webster, A.B., Jordaan, J., Prys-Jones, T.O., Ganswindt, A., De Jager, P., Doughty, C.E., 2021. Hyenas play unique ecosystem role by recycling key nutrients in bones. *Afr. J. Ecol.* <https://doi.org/10.1111/aje.12907>.
- Abrams, G., Bello, S.M., Di Modica, K., Pirson, S., Bonjean, D., 2014. When Neanderthals used cave bear (*Ursus spelaeus*) remains: Bone retouchers from unit 5 of Sceldina Cave (Belgium). *Quatern. Int.* 326, 274–287.
- Agustí, B., Alcalde, G., Güell, A., I Plans, N.J.-M., Rueda, J. M., Batlle, X.T. 1991. La cova 120, parada de caçadors-recol·lectors del paleolític mitjà. *Revista de prehistòria i protohistòria, Cypsela*, pp. 7–20.
- Airvaux, J., Beauval, C., Primault, J., 2012. Le Site du Moustérien récent de La Ganne à Mazerolles et les repaires d’hyènes des Plumettes et des Rochers de Villeneuve à Lussac-les-Châteaux (Vienne). *Hypothèses sur la relation Homme – Carnivore. Bulletin Préhistoire du Sud-Ouest* 20 (1), 3–37.
- Aisher, A., Damodaran, V., 2016. Introduction: Human-nature Interactions through a Multispecies Lens. *Conserv. Soc.* 14 (4), 293–304.
- Albarella, U., Dobney, K.M., Ervynck, A., Rowley-Conwy, P. (Eds.), 2007. *Pigs and humans: 10,000 years of interaction.* Oxford University Press, Oxford.
- Altuna, J., Mariezkurrena, K., Elorza, M. 2001. Arqueozoología de los niveles paleolíticos de la Cueva de Abauntz (Arraiz Navarra). *Estudios de prehistoria y arqueología* 2001-2002, Saldvie, pp. 1-26.
- Álvarez-Laó, D.J., Rivals, F., Sánchez-hernández, C., Blasco, R., Rosell, J., 2017. Ungulates from Teixoneres Cave (Moia, Barcelona, Spain): Presence of cold-adapted elements in NE Iberia during the MIS 3. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 466, 287–302.
- Ames, C.J., Riel-Salvatore, J., Collins, B.R., 2013. Why we need an alternative approach to the study of modern human behaviour. *Can. J. Archaeol.* 37 (1), 21–47.
- Anderson, B., 1983. *Imagined Communities: Reflections on the Origin and Spread of Nationalism.* Verso, London/New York.
- Anderson, B., Harrison, P. (Eds.), 2010. *Taking-Place: Non-Representational Theories and Geography.* Ashgate, Farnham.

- Anderson, K., Perrin, C., 2018. "Removed from nature": the modern idea of human exceptionality. *Environ. Humanit.* 10 (2), 447–472.
- Anderson, L., Lejay, M., Brugal, J.-P., Costamagno, S., Heckel, C., de Araujo Igreja, M., Pradeau, J.-V., Salomon, H., Sellami, F., Théry-Parisot, I., Barshay-Szmidt, C., Mensan, R., Bon, F., 2018. Insights into Aurignacian daily life and camp organization: The open-air site of Régismont-le-Haut. *Quaternary International* 498, 69–98.
- Angevin, R., Langlais, M., 2009. In: *Du matériel au spirituel*, pp. 223–242.
- Angheliu, M., 2014. Stasis and change in Paleolithic times. A brief assessment of the Lower and Middle Paleolithic evolutionary dynamics. *Studii de Preistorie* 11, 19–31.
- Arceredillo Alonso, D., Gómez-Olivencia, A., San Pedro-Calleja, Z., 2013. La fauna de macromamíferos de los niveles pleistocenos de la cueva de Arlanpe (Lemoa, Bizkaia). In: Ríos -Garaizar, J., Garate Maidagan, D., Gómez-Olivencia, A. (eds.) *La cueva de Arlanpe (Lemoa): ocupaciones humanas desde el Paleolítico Medio antiguo hasta la Prehistoria reciente*. Bizkaiko Foru Aldundia, Bilbao, pp. 123–160.
- Arceredillo, D., Brugal, J.-P., Peyrouse, J.-B., Aubry, T., 2018. Paléolithique moyen et supérieur à Buraca Escura (Redinha, Pombal, Portugal): comparaison taphonomique et archéozoologique. *Quaternaire* 29 (1), 53–60.
- Arluke, A., Sanders, C., 2008. *Between the Species: A Reader in Human-Animal Relationships*. Pearson, Boston.
- Armand, D., 1998. La faune de la grotte Bourgeois-Delaunay (Commune de la Chaise de Vouthon, Charente). Résultats préliminaires. *Paléo* 10, 77–86.
- Armstrong Oma, K., 2018. *Humanity and Animality*. In: López Varela, S.L. (Ed.), *The Encyclopedia of Archaeological Sciences*. Wiley & Sons, New York. <https://doi.org/10.1002/9781119188230.saseas0312>.
- Armstrong Oma, K., Goldhahn, J., 2020. Introduction: human-animal relationships from a long-term perspective. *Curr. Swedish Archaeol.* 28 (1), 11–22.
- Arribas, A., Palmqvist, P., 1999. On the ecological connection between sabre-tooths and hominids: faunal dispersal events in the lower pleistocene and a review of the evidence for the first human arrival in Europe. *J. Archaeol. Sci.* 26, 571–585.
- Arsuaga, J.L., Villaverde, V., Quam, R., Martínez, I., Carretero, J.M., Lorenzo, C., Gracia, A., 2007. New Neandertal remains from Cova Negra (Valencia, Spain). *J. Hum. Evol.* 52, 31–58.
- Arsuaga, J.L., Baquedano, E., Pérez-González, A., 2011. Neandertal and Carnivore Occupations in Pinilla del Valle Sites (Community of Madrid, Spain). In: Oosterbeek, L., Fidalgo, C. (Eds.), *Miscellanea. Archaeopress, Oxford*, pp. 111–119.
- Arsuaga, J.L., Baquedano, E., Pérez-González, A., Sala, N., Quam, R.M., Rodríguez, L., García, R., García, N., Álvarez-Lao, D.J., Laplana, C., Huguet, R., Sevilla, P., Maldonado, E., Blain, H.-A., Ruiz-Zapata, M.B., Sala, P., Gil-García, M.J., Uzquiano, P., Pantoja, A., Márquez, B., 2012. Understanding the ancient habitats of the last-interglacial (late MIS 5) Neanderthals of central Iberia: Paleoenvironmental and taphonomic evidence from the Cueva del Camino (Spain) site. *Quat. Int.* 275, 55–75.
- Arroyo-Kalin, M., 2016. Landscaping, Landscape Legacies, and Landesque Capital in Pre-Columbian Amazonia. In: Isendahl, C., Stump, D. (Eds.), *The Oxford Handbook of Historical Ecology and Applied Archaeology*. Oxford Handbooks Online. <https://doi.org/10.1093/oxfordhb/9780199672691.013.16>.
- Auguste, P., 1992. Étude archéozoologique des grands mammifères du site pléistocène moyen de Biache-Saint-Vaast (Pas-de-Calais, France): apports biostratigraphiques et paléontographiques. *Anthropol* 96, 49–70.
- Auguste, P., 1995. Chasse et charognage au paléolithique moyen: L'apport du gisement de Biache-Saint-Vaast (Pas-de-Calais). *Bulletin de la Société Préhistorique Française* 92, 155–167.
- Baca, M., Mackiewicz, P., Stankovic, A., Popoviaz, D., Stefaniak, K., Czarnogórska, K., Nadachowski, A., Gasirowski, M., Hercman, H., Wegleński, P., 2014. Ancient DNA and dating of cave bear remains from Niedzwiedzia Cave suggest early appearance of *Ursus ingressus* in Sudetes. *Quat. Int.* 339–340, 217–223.
- Bailey, G., Galanidou, N., 2009. Caves, palimpsests and dwelling spaces: examples from the Upper Palaeolithic of south-east Europe. *World Archaeology* 41 (2), 215–241.
- Banks, W.E., Moncel, M.-H., Raynal, J.-P., Cobos, M.E., Romero-Alvarez, D., Woillez, M.-N., Faivre, J.-P., Gravina, B., d'Errico, F., Locht, J.-L., Santos, F., 2021. An ecological niche shift for Neandertal populations in Western Europe 70,000 years ago. *Sci. Rep.* 11, 5346.
- Barsh, R.L., Marlor, C., 2003. Driving Bison and Blackfoot Science. *Human Ecology* 31 (4), 571–593.
- Barton, R.N.E., Currant, A.P., Fernandez-Jalvo, Y., Finlayson, J.C., Goldberg, P., Macphail, R., Pettitt, P., Stringer, C.B., 1999. Gibraltar Neanderthals and results of recent excavations in Gorham's, Vanguard and Ibex Caves. *Antiquity* 73, 13–23.
- Barton, R.N.E., 2012. The lithic artefact assemblages of Vanguard Cave. In: Barton, R.N.E., Stringer, C.B., Finlayson, J.C. (Eds.), *Neanderthals in Context: a report of the 1995–1998 excavations at Gorham's and Vanguard Caves, Gibraltar*. Oxford University School of Archaeology, Oxford, pp. 243–252.
- Barton, P.S., Cunningham, S.A., Lindenmayer, D.B., Manning, A.D., 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia* 171 (4), 761–772.
- Baumann, C., Bocherens, H., Drucker, D.G., Conard, N.J., 2020. Fox dietary ecology as a tracer of human impact on Pleistocene ecosystems. *PLoS ONE* 15 (7), e0235692.
- Baynes-Rock, M., 2013. Life and death in the multispecies commons. *Social Sci. Inform.* 52 (2), 210–227.
- Baynes-Rock, M., 2015a. Among the Bone Eaters. Encounters with Hyenas in Harar. The Pennsylvania State University Press, Pennsylvania.
- Baynes-Rock, M., 2015b. Converging on Ancient Bones: A Review of the Evidence for the Close Relatedness of Humans (*Homo sapiens*) and Spotted Hyenas (*Crocuta crocuta*). *HUMANIMALIA* 7 (1). <https://doi.org/10.52537/humanimalia.9980>.
- Baynes-Rock, M., 2016. The ontogeny of hyena representations among the harari people of Ethiopia. *Africa* 86 (2), 288–304.
- Bawaka Country, Wright, S., Suchet-Pearson, S., Lloyd, K., Burarrwanga, L., Ganambarr, R., Ganambarr-Stubbs, M., Ganambarr, B., Maymuru, D., 2015. Working with and learning from Country: decentering human author-ity. *Cultural geographies* 22 (2), 269–283.
- Beauval, C., Morin, E., 2010. Les repaires d'hyènes du Lussacois (Lussac-les-Châteaux, Vienne, France): Apport des sites des Plumettes et des Rochers-de-Villeneuve. In: Buisson-Catil, J., Primault, J. (Eds.), *Préhistoire entre Vienne et Charente*. Association des Publications Chauvinoises Chauvigny, Hommes et sociétés du Paléolithique, pp. 175–190.
- Beauval, C., Maureille, B., Lacrampe-Cuyaubère, F., Serre, D., Peressinotto, D., Bordes, J.-G., Cocharad, D., Couchoud, I., Dubrasquet, D., Laroulandie, V., Lenoble, A., Mallye, J.-B., Pasty, S., Primault, J., Rohland, N., Pääbo, S., Trinkaus, E., 2005. A late Neandertal femur from Les Rochers-de-Villeneuve, France. *PNAS* 102, 7085–7090.
- Becam, G., Chevalier, T., 2017. Neandertal features of the deciduous and permanent teeth from Portel-Oest Cave (Ariège, France). *Am. J. Phys. Anthropol.* 168, 45–69.
- Bednarik, R.G., 1994. Art origins. *Anthropos* 89, 169–180.
- Bekoff, M., 2002. *Minding Animals: Awareness, Emotions, and Heart*. Oxford University Press, New York.
- Bennett, C.F., 1960. Cultural animal geography: an inviting field of research. *Professional Geographer* 12 (5), 12–14.
- Benson-Amram, S., Holecamp, K.E., 2012. Innovative problem solving by wild spotted hyenas. *Proc. Roy. Soc. Lond. B* 279, 4087–4095.
- Bernard, E., 2019. *Néandertaliens et grands carnivores au stade 3: étude du site de Cassenade (Dordogne)*. Unpublished Master Thesis, University of Toulouse, Toulouse.
- Bertacchi, A., Starkovich, B.M., Conard, N.J., 2021. The Zooarchaeology of Sirgenstein Cave: A Middle and Upper Paleolithic site in the Swabian Jura, SW Germany. *J. Paleol. Archaeol.* 4, 7. <https://doi.org/10.1007/s41982-021-00075-8>.
- Betts, M.W., Hardenberg, M., Stirling, I., 2015. How Animals Create History: Relational Ecology and the Dorset-Polar Bear Connection. *Am. Antiq.* 80 (1), 89–112.
- Bicho, N., Cardoso, J.L., 2010. Paleolithic occupations and lithic assemblages from Fuminha Cave, Peniche (Portugal). *Revista de Prehistoria y Arqueología, Zephyrus*, pp. 17–38.
- Binford, L.R., 1989. *Debating Archaeology*. Studies in Archaeology. Academic Press, San Diego.
- Binford, L.R., Mills, M.G.L., Stone, N.M., 1988. Hyena scavenging behavior and its implications for the interpretation of faunal assemblages from FLK 22 (the Zinj Floor) at Olduvai Gorge. *J. Anthropol. Archaeol.* 7, 99–135.
- Bird, D.M., Varland, D., Negro, J.J. (Eds.) 1996. *Raptors in Human Landscapes. Adaptations to built and cultivated environments*. Academic Press, London et al.
- Bird-David, N., 1990. The giving environment: another perspective on the economic system of gatherer-hunters. *Curr. Anthropol.* 31 (2), 189–196.
- Bird-David, N., 1994. Sociality and immediacy: or, past and present conversations on bands. *Man* 29 (3), 583–603.
- Bird-David, N., 1999. "Animism" revisited: personhood, environment, and relational epistemology. *Curr. Anthropol.* 40 (1), 67–91.
- Bird-David, N., 2006. Animistic epistemology: why do some hunter-gatherers not depict animals. *Ethnos* 71 (1), 33–50.
- Bird-David, N., 2017a. *Us, Relatives. Scaling and Plural Life in A Forager World*. University of California Press, Oakland.
- Bird-David, N., 2017b. Before Nation. *Scale-Blind Anthropology and Foragers' Worlds of Relatives*. *Current Anthropology* 58 (2), 209–226.
- Bird-David, N., 2018. Size matters! The scalability of modern hunter-gatherer animism. *Quat. Int.* 464, 305–314.
- Bird-David, N., 2019. Where have all the kin gone? On hunter-gatherers' sharing, kinship and scale. In: Lavi, N., Friesem, D.E. (Eds.), *Towards a Broader View of Hunter-Gatherer Sharing*. McDonald Institute for Archaeological Research, Cambridge, pp. 15–24.
- Bird-David, N., Naveh, D., 2008. Relational Epistemology, Immediacy, and Conservation: Or, What Do the Nayaka Try to Conserve? *J. Study Religion Nat. Cult.* 2 (1), 55–73.
- Birkner, F., 1915. *Der Eiszeitmensch in Bayern. Beiträge zur Anthropologie und Urgeschichte Bayerns* 105–134.
- Birks, H.J.B., Willis, K.J., 2008. Alpines, trees, and refugia in Europe. *Plant Ecol. Divers.* 1 (2), 147–160.
- Blanco, G., Sánchez-Marco, A., Negro, J., 2021. Night capture of roosting cave birds by Neanderthals: an actualistic approach. *Front. Ecol. Evolution* 9, 733062.
- Blasco, R., Rosell, J., Rufá, A., Marco, A.S., Finlayson, C., 2016. Pigeons and choughs, a usual resource for the Neanderthals in Gibraltar. *Quat. Int.* 421, 62–77.
- Blumenshine, R.J., 1987. Characteristics of an early hominid scavenging niche. *Curr. Anthropol.* 28, 383–407.
- Bocherens, H., 2011. Diet and Ecology of Neanderthals: Implications from C and N Isotopes. In: Conard, N.J., Richter, J. (Eds.), *Neandertal Lifeways, Subsistence and Technology. One Hundred Fifty Years of Neandertal Study*, Springer, Dordrecht, pp. 73–85.
- Bocherens, H., 2018. The Rise of the Anthroposphere since 50,000 Years: An Ecological Replacement of Megaherbivores by Humans in Terrestrial Ecosystems? *Front. Ecol. Evol.* 6 (3), 2018. <https://doi.org/10.3389/fevo.2018.00003>.
- Bocquet-Appel, J.-P., Degioanni, A., 2013. Neandertal demographic estimates. *Curr. Anthropol.* 54 (8), 202–213.
- Boivin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlanson, J.M., Denham, T., Petraglia, M.D., 2016. Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. *Proc. Natl. Acad. Sci. USA* 113 (23), 6388–6396.
- Bolus, M., 2004a. Der Übergang vom Mittel- zum Jungpaläolithikum in Europa. Eine Bestandsaufnahme unter besonderer Berücksichtigung Mitteleuropas. *Germania* 82, 1–54.

- Bolus, M. 2004b. Settlement analysis of sites of the Blattspitzen complex in central Europe. In: Conard, N. (Ed.), *Settlement dynamics of the Middle Paleolithic the Middle Stone Age*, Vol. II. Kerns, Tübingen, pp. 201–226.
- Bolus, M., Schmitz, R., 2006. *Der Neandertaler*. Thorbecke, Stuttgart.
- Bon, F., 2015. À la croisée des chemins (crossroad traffic). *P@lethnologie* 7, 8–18.
- Bourrillon, R., White, R., 2015. Early Aurignacian Graphic Arts in the Vézère Valley. *P@lethnologie* 7, 118–137.
- Boyd, B., 2017. Archaeology and human-animal relations: thinking through anthropocentrism. *Ann. Rev. Anthropol.* 46, 299–316.
- Boydston, E.E., Kapheim, K.M., Watt, H.E., Szykman, M., Holekamp, K.E., 2003. Altered behaviour in spotted hyenas associated with increased human activity. *Anim. Conserv.* 6, 207–219.
- Böttcher, R., Çep, B., Kind, C.-J., Mörike, D., Pawlik, A., Rähle, W., Steppan, K., Torke, W., Ziegler, R., 2000. Kogelstein – eine mittelpaläolithische Fundstelle bei Schelklingen/Schmiechen. *Fundberichte in Baden-Württemberg* 24, 7–176.
- Bradley, R., 2000. *An Archaeology of Natural Places*. Routledge, London.
- Brantingham, P.J., 1998. Hominid-carnivore co-evolution and invasion of the predatory guild. *J. Anthropol. Archaeol.* 17, 327–353.
- Bratlund, B., 1999. Taubach revisited. *Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz* 46, 67–174.
- Brown, S., Wang, N., Oertle, A., Kozlikin, M.B., Shunkov, M.V., Derevianko, A.P., Comesky, D., Jope-Street, B., Harvey, V.L., Chowdhury, M.P., Buckley, M., Higham, T., Douka, K., 2021. Zooarchaeology through the lens of collagen fingerprinting at Denisova Cave. *Sci. Rep.* 11, 15457.
- Brittain, M., Overton, N., 2013. The significance of others: a prehistory of rhythm and interspecies participation. *Society & Animals* 21 (2), 134–149.
- Brugal, J.-P., 2010. Carnivores pléistocènes (hyénidés, Canidés, Félidés) dans les grottes du Portugal. In: 1<sup>o</sup> Reunión de científicos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica. Museo Arqueológico Regional, Madrid, pp. 91–106.
- Brugal, J.-P., Jaubert, J., 1991. Les gisements paléontologiques pléistocènes à indices de fréquentation humaine: un nouveau type de comportement de prédation? *Paléo* 3, 15–41.
- Brugal, J.-P., Fosse, P., 2004. Carnivores et Hommes au Quaternaire en Europe de l'Ouest. *Revue de Paléobiologie*, Genève 23 (2), 575–595.
- Brugal, J.-P., Argant, J., Crispim, J.A., Figueiredo, S., Serra, A.M., Palmqvist, P., 2012. The complex carnivore-rich assemblages from furninha (Peniche, Portugal): a multidisciplinary approach. *J. Taphonomy* 10 (3–4), 417–438.
- Brugal, J.-P., Argant, A., Boudadi-Maligne, M., Crégut-Bonnoure, E., Croitor, R., Fernandez, P., Fourvel, J.-B., Fosse, P., Guadelli, J.-L., Labe, B., Magniez, P., Uzunidis, A., 2020. Pleistocene herbivores and carnivores from France: An updated overview of the literature, sites and taxonomy. *Annales de Paléontologie* 106 (2), 102384.
- Brumm, A., Oktaviana, A.A., Burhan, B., Hakim, B., Lebe, R., Zhao, J.-X., Sulistyarto, P. H., Ririmasse, M., Adhityatama, S., Samantir, I., Aubert, M., 2021. Oldest cave art found in Sulawesi. *Sci. Adv.* 7, eabd4648.
- Bruno, J., Stachowicz, J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18, 119–125.
- Buisson, D., Delporte, H., 1990. Existence du Castelperronien à Brassempouy (Landes). In: Farizy, C. (Ed.), *Paléolithique moyen récent et Paléolithique supérieur ancien en Europe*. A.P.R.A.I.F., Nemours, pp. 189–193.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania. *Curr. Anthropol.* 27 (5), 431–442.
- Camarós, E., Cueto, M., Lorenzo, C., Villaverde, V., Rivals, F., 2016. Large carnivore attacks on hominins during the Pleistocene: a forensic approach with a Neanderthal example. *Archaeol. Anthropol. Sci.* 8 (3), 635–646.
- Camarós, E., Cueto, M., Teira, L., Münzel, S.C., Plassard, F., Arias, P., Rivals, F., 2017. Bears in the scene: Pleistocene complex interactions with implications concerning the study of Neanderthal behavior. *Quatern. Int.* 435, 237–246.
- Campmans, E., 2017. Integrating Human-Animal Relationships into New Data on Aterian Complexity: a Paradigm Shift for the North African Middle Stone Age. *African Archaeol. Rev.* 34, 469–491.
- Candeia, M., 2010. I Fell in Love with Carlos the Meerkat: Engagement and detachment in human-animal relations. *Am. Ethnol.* 37 (2), 241–258.
- de Carvalho Cabral, D., 2021. Horizontality, negotiation, and emergence: toward a philosophy of environmental history. *Historia Ambiental Latinoamericana Y Caribeña (HALAC)* 11 (3), 235–258.
- Carrión, J.S., Finlayson, C., Fernández, S., Finlayson, G., Allué, E., López-Sáez, J.A., López-García, P., Gil-Romera, G., Bailey, G., González-Sampériz, P., 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations: palaeoecological investigations in Gorham's Cave (Gibraltar) in the context of the Iberian Peninsula. *Quat. Sci. Rev.* 27, 2118–2135.
- Carrión, J.S., Ochando, J., Fernández, S., Blasco, R., Rosell, J., Munuera, M., Amorós, G., Martín-Lerma, I., Finlayson, S., Giles, F., 2018. Last Neanderthals in the warmest refugium of Europe: Palynological data from Vanguard Cave. *Rev. Palaeobot. Palynol.* 259, 63–80.
- Carrión, J.S., Fernández, S., Jiménez-Arenas, J.M., Munuera, M., Ochando, J., Amorós, G., Ponce De León, M., Zollikofer, C., Martín-Lerma, I., Toro-Moyano, I., Hajdas, I., Walker, M.J., 2019. The sequence at Carhuela Cave and its potential for research into Neanderthal ecology and the Mousterian in southern Spain. *Quat. Sci. Rev.* 217, 194–216.
- Castaña, P., 2005. Revisión actualizada de las faunas de macromamíferos del Würm antiguo en la Región Cantábrica. In: Montes Barquín, R., Lasheras Corrachaga, J.A. (Eds.), *Actas de la Reunión científica: Neandertales Cantábricos*. Estado de la cuestión, Ministerio de Cultura, Madrid, pp. 201–207.
- Castel, J.-C., Discamps, E., Soulier, M.-C., Sandgathe, D., Dibble, H., McPherron, S.J.P., Goldberg, P., Turq, A., 2017. Neandertal subsistence strategies during the Quina Mousterian at Roc de Marsal (France). *Quat. Int.* 433, 140–156.
- Cavanhié, N., 2011. L'ours qui a vu l'homme? Étude archéozoologique et taphonomique du site paléolithique moyen de Regourdou (Montignac, Dordogne, France). *PALEO: Revue d'archéologie préhistorique* 21, 39–63.
- Çep, B., Schürch, B., Münzel, S.C., Frick, J.A., 2021. Adaptive capacity and flexibility of the Neanderthals at Heidschmiede (Swabian Jura) with regard to core reduction strategies. *PLoS ONE* 16 (9), e0257041.
- Chang, M.L., Nowell, A., 2020. Conceiving of them, before there was only us. In: Supernant, K., Lyons, N., Baxter, J., Atalay, S. (Eds.), *Archaeologies of the Heart*. Springer, New York, pp. 205–223.
- Childe, V.G., 1936. *Man Makes Himself*. Watts and Co., London.
- Chmielewski, W., Kowalski, K., Madeyska-Niklewska, T., Sych, L., 1967. Wyniki badań osadów Jaskini Koziařnia w Saspowie, pow. Olkusz, Państwowe Wydawnictwo Naukowe, Kraków.
- Churchill, S.E., 2014. *Thin On The Ground: Neandertal Biology, Archeology, and Ecology*. Wiley Blackwell, Chichester.
- Clark, D., Artelle, K., Darimont, C., Housty, W., Tallio, C., Neasloss, D., Schmidt, A., Wiget, A., Turner, N., 2021. Grizzly and polar bears as nonconsumptive cultural keystone species. *FACETS* 6, 379–393.
- Cleghorn, E.J., 2017. Waste Not: A Reexamination of Neanderthal Hunting Strategies and Their Relationships with Animals. Unpublished M.A. Thesis, University of York.
- Clot, A., 1970. Note préliminaire sur la grotte de la Carrière, à Gerde (Hautes-Pyrénées). *Bulletin de la Société préhistorique française. Études et travaux* 67 (2), 427–434.
- Clottes, J., Azéma, M., 2005. Les images des félins de la grotte Chauvet. *Bulletin de la Société préhistorique française* 102 n°1, 173–182.
- Clucas, B., Marzluff, J.M., 2011. Coupled Relationships between Humans and other Organisms in Urban Areas. In: Niemelä, J., Breuste, J.H., Elmqvist, T., Guntenspergen, G., James, P., McIntyre, N.E. (Eds.), *Urban ecology: patterns, processes, and applications*. Oxford University Press, New York, pp. 135–147.
- Coil, R.A., 2016. Spatial approaches to site formation and carnivore-hominin interaction at Dmanisi, Georgia. University of Minnesota. Doctoral Dissertation.
- Coleman, E.B., Hartney, C., Alderton, Z., 2013. Defining 'Social Aesthetics'. *Aesthetics* 23 (1), 1–11.
- Conard, N.J., Bolus, M., Münzel, S.C., 2012. Middle Paleolithic land use, spatial organization and settlement intensity in the Swabian Jura, southwestern Germany. *Quat. Int.* 247, 236–245.
- Connell, C., 2011. *An Archaeology of Materials. Substantial Transformations in Early Prehistoric Europe*. Routledge, New York/London.
- Cooper, L.P., Thomas, J.S., Beamish, M.G., Gouldwell, A., Colcutt, S.N., Williams, J., Jacobi, R.M., Currant, A., Higham, T.E.G., 2011. An Early Upper Palaeolithic Open-air Station and Mid-Devensian Hyaena Den at Grange Farm, Glaston, Rutland, UK. *Proc. Prehist. Soc.* 78, 73–93.
- Corry, S., 2011. *Tribal Peoples For Tomorrow's World*. Freeman Press, Cookhill.
- Costamagno, S., Beauval, C., Lange-Badré, B., Vandermeersch, B., Mann, A., Maureille, B., 2005. Homme ou carnivores? Protocole d'étude d'ensembles osseux mixtes: l'exemple du gisement moustérien des Pradelles (Marillac-le-Franc, Charente). *Archaeofauna* 14, 43–68.
- Costamagno, S., Liliane, M., Cédric, B., Bernard, V., Bruno, M., 2006. Les Pradelles (Marillac-le-Franc, France): A mousterian reindeer hunting camp? *J. Anthropol. Archaeol.* 25 (4), 466–484.
- Costamagno, S., Gourichon, L., Dupont, C., Dutour, O., Vialou, D. (Eds.), 2018a. Animal symbolisé, animal exploité: du Paléolithique à la Protohistoire. CTHS, Paris.
- Crezzini, J., Boscato, P., Ricci, S., Ronchitelli, A., Spagnolo, V., Boschin, F., 2016. A spotted hyena den in the Middle Palaeolithic of Grotta Paglicci (Gargano promontory, Apulia, Southern Italy). *Archaeol. Anthropol. Sci.* 8, 227–240.
- Costamagno, S., Bourguignon, L., Soulier, M.-C., Meignen, L., Beauval, C., Rendu, W., Mussini, C., Mann, A., Maureille, B., 2018b. Bone Retouchers and site function in the Quina Mousterian: the case of Les Pradelles (Marillac-le-Franc, France). In: Hutson, J.M., García-Moreno, A., Noack, E.S., Turner, E., Villaluenga, A., Gaudzinski-Windheuser, S. (Eds.), *Retouching the Palaeolithic: Becoming Human and the Origins of Bone Tool Technology*. Verlag des Römisch-Germanischen Zentralmuseums, Mainz, pp. 165–195.
- Crumley, C.L., 1994. *Historical ecology: cultural knowledge and changing landscapes*. School of American Research Press, Santa Fe.
- Cueto, M., Camarós, E., Castaños, P., Ontañón, R., Arias, P., 2016. Under the Skin of a Lion: Unique Evidence of Upper Paleolithic Exploitation and Use of Cave Lion (*Panthera spelaea*) from the Lower Gallery of La Garma (Spain). *PLoS ONE* 11 (10), e0163591.
- Currant, A., Jacobi, R., 2001. A formal mammalian biostratigraphy for the Late Pleistocene of Britain. *Quat. Sci. Rev.* 20, 1707–1716.
- Dalén, L., Orlando, L., Shapiro, B., Brandström-Durling, M., Quam, R., Gilbert, M.T.P., Díez Fernández-Lomana, J.C., Willerslev, E., Arsuaga, J.L., Götherström, A., 2012. *Mol. Biol. Evol.* 29 (8), 1893–1897.
- Daschek, E.J., Mester, Z., 2020. A site with mixed occupation: Neanderthals and carnivores at Erd (Hungary). *J. Archaeol. Sci.: Rep.* 29, 102116.
- Daujeard, C., Abrams, G., Germonpré, M., Le Pape, J.-M., Wampach, A., Di Monica, K., Moncel, M.-H., 2016. Neanderthal and animal karstic occupations from southern Belgium and south-eastern France: Regional or common features? *Quat. Int.* 411, 179–197.
- Daujeard, C., Vettese, D., Britton, K., Béarez, P., Boubles, N., Crégut-Bonnoure, E., Desclaux, E., Lateur, N., Pike-Tay, A., Rivals, F., Allué, E., Chacón, M.G., Puaud, S., Richard, M., Courty, M.-A., Gallotti, R., Hardy, B., Bahain, J.J., Falguères, C., Pons-Branchu, E., Valladas, H., Moncel, M.-H., 2019. Neanderthal selective hunting of

- reindeer? The case study of Abri du Maras (south-eastern France). *Archaeol. Anthropol. Sci.* 11, 985–1011.
- Daura, J., Sanz, M., 2014. Cova del Gegant (Sitges, Barcelona). In: Ramos, R.S. (Ed.), *Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait*. Universidad de Burgos, Servicio de Publicaciones, Burgos, pp. 276–280.
- Daura, J., Sanz, M., Allué, E., Vaquero, M., López-García, J.M., Sánchez-Marco, A., Domènech, R., Martinelli, J., Carrión, J.S., Ortiz, J.E., Torres, T., Arnold, L.J., Benson, A., Hoffmann, D.L., Skinner, A.R., Julià, R., 2017. Palaeoenvironments of the last Neanderthals in SW Europe (MIS 3): Cova del Coll Verdaguer (Barcelona, NE of Iberian Peninsula). *Quat. Sci. Rev.* 177, 34–56.
- Davis, S.J.M., Robert, I., Zilhão, J., 2007. Caldeirão cave (Central Portugal) – whose home? Hyena, man, bearded vulture... *Courier – Forschungsinstitut Senckenberg* 259, 213–226.
- Debénath, A., Jelinek, A.J., 1998. Nouvelles Fouilles à la Quina (Charente). *Gallia Préhistoire* 40, 29–74.
- Delagnes, A., Rendu, W., 2011. Shifts in Neandertal mobility, technology and subsistence strategies in western France. *J. Archaeol. Sci.* 38 (8), 1771–1783.
- Delagnes, A., Tournepiche, J.-F., Armand, D., Desclaux, E., Diot, M.F., Ferrier, C., Le Fillâtre, V., Vandermeersch, B., 1999. Le gisement Pléistocène moyen et supérieur d'Artenac (Saint-Mary, Charente): premier bilan interdisciplinaire. *Bulletin de la Société préhistorique française* 96 (4), 469–496.
- De la Torre, I., Martínez-Moreno, J., Mora, R., 2013. Change and stasis in the Iberian middle paleolithic considerations on the significance of mousterian technological variability. *Curr. Anthropol.* 54 (8), 320–336.
- De Lombera-Hermida, A., Rodríguez, X., Fábregas-Valcarlos, R., 2014. Cova Eirós archaeo-palaeontological site, Triacastela, Lugo. In: Ramos, R.S. (Ed.), *Pleistocene and Holocene Hunter-Gatherers in Iberia and the Gibraltar Strait*. Current Archaeological Record. Universidad de Burgos, Servicio de Publicaciones, Burgos, pp. 18–25.
- De Los Terreros, J.Y.S., 2007. Nuevas contribuciones en el comportamiento cinegético de la Cueva de Amalda. *Munibe Antropología-Arkeologia* 43–88.
- DeMello, M., 2012. *Animals and Society: An Introduction to Human-Animal Studies*. Columbia University Press, New York.
- Demuth, B., 2019. *Floating Coast: An Environmental History of the Bering Strait*. W.W. Norton & Company, New York.
- d'Errico, F., Doyon, L., Colagè, I., Queffelec, A., Le Vraux, E., Giacobini, G., Vandermeersch, B., Maureille, B., 2018. From number sense to number symbols. An archaeological perspective. *Philos. Trans. R. Soc. B: Biol. Sci.* 373 (1740), 20160518.
- Descola, P., 1994. In the Society of Nature: A Native Ecology in Amazonia. Cambridge University Press, Cambridge, Translated by N. Scott.
- Descola, P., 1996. Constructing natures: symbolic ecology and social practice. In: Descola, P., Pálsson, G. (Eds.), *Nature and Society. Anthropological Perspectives*, Routledge, London, pp. 82–102.
- Descola, P., 2005. *Par-delà nature et culture*. Gallimard, Paris.
- Descola, P., 2010a. Cognition, Perception and Worlding. *Interdisc. Sci. Rev.* 35 (3–4), 334–340.
- Descola, P., 2010b. Diversité des natures, diversité des cultures. Bayard, Paris.
- Descola, P., 2014. Modes of being and forms of predication. *HAU: J. Ethnogr. Theory* 4 (1), 271–280.
- Descola, P., Pálsson, G. (Eds.), 1996. *Nature and Society. Anthropological Perspectives*. Routledge, London.
- De Soler, B.G., Soto, M., Vallverdú, J., Vaquero, M., Bargalló, A., Chacón, M.G., Romagnoli, F., Carbonell, E., 2020. Neandertal lithic procurement and mobility patterns through a multi-level study in the Abric Romaní site (Capellades, Spain). *Quat. Sci. Rev.* 237, 106315.
- Dibble, H.L., Aldeias, V., Goldberg, P., McPherron, S.P., Sandgathe, D., Steele, T.E., 2015. A critical look at evidence from La Chapelle-aux-Saints supporting an intentional Neandertal burial. *J. Archaeol. Sci.* 53, 649–657.
- Dibble, H., Berna, F., Goldberg, P., McPherron, S., Mentzer, S., Niven, L., Richter, D., Sandgathe, D., Théry-Pariset, L., Turq, A., 2009. A preliminary report on Pech de l'Azé IV, layer 8 (Middle Paleolithic, France). *PaleoAnthropology* 2009, 182–219.
- Diedrich, C.G., 2009. Steppe lion remains imported by Ice Age spotted hyenas into the Late Pleistocene Perick Caves hyena den in northern Germany. *Quat. Res.* 71 (3), 361–374.
- Diedrich, C.G., 2011. Pleistocene *Panthera leo spelaea* (Goldfuss 1810) remains from the Balve cave (NW Germany) – a cave bear, hyena den and middle palaeolithic human cave - and review of the Sauerland Karst lion cave sites. *Quaternaire: Revue de l'Association française pour l'étude du Quaternaire* 22 (2), 105–127.
- Diedrich, C.G., 2012. Late Pleistocene *Crocota crocuta spelaea* (Goldfuss, 1823) clans as przewalski horse hunters and woolly rhinoceros scavengers at the open air commuting den and contemporary Neandertal camp site Westeregeln (central Germany). *J. Archaeol. Sci.* 39, 1749–1767.
- Diedrich, C.G., 2014. Ice Age spotted hyenas as Neandertal exhumers and scavengers in Europe. *Chronicles of Science* 1 (1), 1–34.
- Diedrich, C.G., 2015. 'Neandertal bone flutes': simply products of Ice Age spotted hyena scavenging activities on cave bear cubs in European cave bear dens. *R. Soc. Open Sci.* 2, 140022.
- Diedrich, C.G., Zák, K., 2006. Prey deposits and den sites of the Upper Pleistocene hyena *Crocota crocuta spelaea* (Goldfuss, 1823) in horizontal and vertical caves of the Bohemian Karst (Czech Republic). *Bulletin of Geosciences* 81, 237–276.
- Di Monica, K., 2010. Les productions lithiques du Paléolithique moyen de Belgique: variabilité des systèmes d'acquisition et des technologies en réponse à une mosaïque d'environnements contrastés. Unpublished Doctoral Dissertation, University of Liège, Liège.
- Di Monica, K., Jungels, C., Hauzeur, A., 2013. What do we know today about the Middle Palaeolithic of Spy? In: Rougier, H., Semal, P. (Eds.), *Spy Cave. 125 years of multidisciplinary research at the Betche aux Rotches (Jemeppe-sur-Sambre, Province of Namur, Belgium)*, Volume 1. Institut royal des Sciences naturelles de Belgique, Brussels, pp. 167–200.
- Discamps, E., 2009. A “hyena event” at the Middle-to-Upper Palaeolithic transition? Preliminary results from South-West of France. In: 1<sup>re</sup> Reunión de científicos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica. Alcalá de Henares, Spain, pp. 510–516.
- Discamps, E., 2011. Hommes et hyènes face aux recompositions des communautés d'Ongulés (MIS 5–3): éléments pour un cadre paléocologique des sociétés du Paléolithique moyen et supérieur ancien d'Europe d'Ouest. University of Bordeaux I. Doctoral Dissertation.
- Discamps, E., 2014. Ungulate biomass fluctuations endured by Middle and Early Upper Paleolithic societies (SW France, MIS 5–3): The contributions of modern analogs and cave hyena paleodemography. *Quat. Int.* 337, 64–79.
- Discamps, E., Delanges, A., Lenoir, M., Tournepiche, J.-F., 2012. Human and Hyena Co-occurrences in Pleistocene sites: Insights from Spatial, Faunal and Lithic Analyses at Camiac and La Chauverie (SW France). *J. Taphonomy* 10 (3–4), 291–316.
- Discamps, E., Bachelier, F., Baillet, M., Sitzia, L., 2019. The Use of Spatial Taphonomy for Interpreting Pleistocene Palimpsests: An Interdisciplinary Approach to the Châtelperronian and Carnivore Occupations at Cassenade (Dordogne, France). *PaleoAnthropology* 2019, 362–388.
- Dominguez-Rodrigo, M., Pickering, T.R., 2017. The meat of the matter: an evolutionary perspective on human carnivory. *Azania: Archaeol. Res. Africa* 52 (1), 4–32.
- Drea, C.M., Carter, A.N., 2009. Cooperative problem solving in a social carnivore. *Anim. Behav.* 78, 967–977.
- Ducarme, F., Luque, G.M., Courchamp, F., 2013. What are “charismatic species” for conservation biologists? *Biosci. Master Rev.* 10, 1–8.
- Dusseldorp, G.L., 2011. Studying Pleistocene Neandertal and cave hyena dietary habits: combining isotopic and archaeozoological analyses. *J. Archaeol. Method Theory* 18 (3), 224–255.
- Dusseldorp, G.L., 2013. Neanderthals and Cave Hyenas: Co-existence, Competition or Conflict? In: Clark, J.L., Speth, J.D. (Eds.), *Zooarchaeology and Modern Human Origins*. Springer, Dordrecht, pp. 191–208.
- Enloe, J.G., 2012. Neanderthals, bears and hyenas, oh my! Competition for exclusive use of space. *J. Taphonomy* 10 (3–4), 193–200.
- Enloe, J.G., David, F., Baryshnikov, G., 2004. Hyenas and Hunters: Zooarchaeological Investigations at Prolom II Cave, Crimea. *Int. J. Osteoarchaeol.* 10, 310–324.
- Estévez, J., 2004. Vanishing carnivores: what can the disappearance of large carnivores tell us about the Neandertal world? *Int. J. Osteoarchaeol.* 14, 190–200.
- Faith, J.T., Rowan, J., Du, A., 2019. Early hominins evolved within non-analog ecosystems. *PNAS* 116 (43), 21478–21483.
- Faivre, J.-P., Gravina, B., Bourguignon, L., Discamps, E., Turq, A., 2017. Late Middle Palaeolithic lithic technocomplexes (MIS 5–3) in the northeastern Aquitaine Basin: Advances and challenges. *Quat. Int.* 433, 116–131.
- Finlayson, B., Warren, G. (Eds.), 2017. *The Diversity of Hunter Gatherer Pasts*. Oxbow Books, Oxford.
- Finlayson, C., 2019. *The Smart Neandertal*. Oxford University Press, Oxford, Bird Catching, Cave Art and the Cognitive Revolution.
- Finlayson, C., Brown, K., Blasco, R., Rosell, J., Negro, J.J., Bortolotti, G.R., Finlayson, G., Sánchez, Marco, A., Giles Pacheco, F., Rodríguez Vidal, J., Carrión, J.S., Fa, D.A., Rodríguez Llanes, J.M., 2012. Birds of a feather: Neandertal exploitation of raptors and corvids. *PLoS ONE* 7 (9), e45927.
- Finlayson, S., Finlayson, C., 2016. The birdmen of the Pleistocene: On the relationship between Neandertals and scavenging birds. *Quat. Int.* 421, 78–84.
- Finlayson, S., Finlayson, G., Giles Guzman, F., Finlayson, C., 2019. Neandertals and the cult of the Sun Bird. *Quat. Sci. Rev.* 217, 217–224.
- Fiore, L., Gala, M., Romandini, M., Cocca, E., Tagliacozzo, A., Peresani, M., 2016. From feathers to food: Reconstructing the complete exploitation of avifaunal resources by Neandertals at Fumane cave, unit A9. *Quat. Int.* 421, 134–153.
- Flas, D., 2008. La transition du Paléolithique moyen au supérieur dans la plaine septentrionale de l'Europe. *Société Royale Belge d'Anthropologie et de Préhistoire*, Brussels.
- Flas, D., 2011. The Middle to Upper Paleolithic transition in Northern Europe: the Lincombian-Ranisian-Jerzmanowician and the issue of acculturation of the last Neandertals. *World Archaeol.* 43, 605–627.
- Flas, D., 2013. Jerzmanowice points from Spy and the issue of the Lincombian-Ranisian-Jerzmanowician. In: Rougier, H., Semal, P. (Eds.), *Spy Cave. 125 Years of Multidisciplinary Research at the Betche Aux Rotches (Jemeppe-Sur-Sambre, Province of Namur, Belgium)*, Société Royale Belge d'Anthropologie et de Préhistoire, Brussels, pp. 217–230.
- Fosse, P., 1997. Variabilité des assemblages osseux créés par l'hyène des cavernes. *Paléo* 9, 15–54.
- Fourvel, J.-B., Fosse, P., Brugal, J.-P., Tournepiche, J.-F., Cregut-Bonnoure, E., 2012. Consumption of Ungulate Long Bones by Pleistocene Hyenas: a Comparative Study. *J. Taphonomy* 10 (3–4), 239–263.
- Fourvel, J.B., Fosse, P., Fernandez, P., Antoine, P.-O., 2015. Large mammals of Fouvent-Saint-Andoche (Haute-Saône, France): a glimpse into a Late Pleistocene hyena den. *Geodiversitas* 37 (2), 237–266.
- Fowles, S., 2018. The evolution of simple society. *Asian Archaeol.* 2 (1), 19–32.
- Frayer, D.W., 2019. Neandertals and the Black Swan. *PaleoAnthropology* 2019, 350–361.
- Frayer, D.W., Radović, J., Radović, D., 2020. Krapina and the case for Neandertal symbolic behavior. *Curr. Anthropol.* 61 (6), 713–731.
- French, J., 2019. The use of ethnographic data in Neandertal archaeological research: recent trends and their interpretative implications. *Hunter Gatherer Res.* 4 (1), 25–49.

- French, J., 2021. *Palaeolithic Europe: A Demographic and Social Prehistory*. Cambridge University Press, Cambridge.
- Frouin, M., Lahaye, C., Mercier, N., Guibert, P., Couchoud, I., Texier, J.-P., Royer, A., Costamagno, S., Beauval, C., Bourguignon, L., Meignen, L., Bordes, J.-G., Seguin, G., Bocherens, H., Lacrampe-Cuyaubère, F., Muth, X., Geigl, E.-M., Grün, R., Garralda, M.D., Vandermeersch, B., Mann, A.E., Maureille, B., 2017. Chronologie du site moustérien de type Quina des Pradelles (Marillac-le-Franc, Charente, France). *Paléo* 28, 117–136.
- Fu, Q., Li, H., Moorjani, P., Jay, F., Slepchenko, S.M., Bondarev, A.A., Johnson, P.L., Aximu-Petri, A., Prüfer, K., de Filippo, C., Meyer, M., Zwyns, N., Salazar-García, D. C., Kuzmin, Y.V., Keates, S.G., Kosintsev, P.A., Razhev, D.I., Richards, M.P., Peristov, N.V., Lachmann, M., Douka, K., Higham, T.F.G., Slatkin, M., Hublin, J.-J., Reich, D., Kelso, J., Viola, T.B., Pääbo, S., 2014. Genome sequence of a 45,000-year-old modern human from western Siberia. *Nature* 514, 445–449.
- Fu, Q., Hajdinjak, M., Moldovan, O.T., Constantin, S., Mallick, S., Skoglund, P., Patterson, N., Rohland, N., Lazaridis, I., Nickel, B., Viola, B., Prüfer, K., Meyer, M., Kelso, J., Reich, D., Pääbo, S., 2015. An early modern human from Romania with a recent Neanderthal ancestor. *Nature* 524, 216–219.
- Fuentes, A., 2010. Natural cultural encounters in Bali: Monkeys, temples, tourists, and ethnoprimateology. *Cult. Anthropol.* 25 (4), 600–624.
- Fuentes, A., 2015. Integrative anthropology and the human niche: toward a contemporary approach to human evolution. *Am. Anthropol.* 117 (2), 302–315.
- Fuentes, A., Wolfe, L.D., 2002. *Primates Face to Face: The Conservation Implications of Human-nonhuman Primate Interconnections*. Cambridge University Press, Cambridge.
- Fuentes, A., Baynes-Rock, M., 2017. Anthropogenic Landscapes, Human Action and the Process of Co-Construction with other Species: Making Anthromes in the Anthropocene. *Land* 6 (15), doi:10.3390/land610015.
- Fuglestedt, I., 2012. The Pioneer Condition on the Scandinavian Peninsula: the Last Frontier of a 'Palaeolithic Way' in Europe. *Norwegian Archaeol. Rev.* 45 (1), 1–29.
- Fuglestedt, I., 2018. *Rock Art and the Wild Mind: Visual Imagery in Mesolithic Northern Europe*. Routledge, New York.
- Gade, D.W., 2006. Hyenas and Humans in the Horn of Africa. *Geogr. Rev.* 96 (4), 609–632.
- Galetti, M., Moléon, M., Jordano, P., Pires, M.M., Guimarães Jr., P.R., Pape, T., Nichols, E., Hansen, D., Olesen, J.M., Munk, M., de Mattos, J.S., Schweiger, A.H., Owen-Smith, N., Johnson, C.N., Marquis, R.J., Svenning, J.-C., 2018. Ecological and evolutionary legacy of megafauna extinctions. *Biol. Rev.* 93 (2), 845–862.
- Gamble, C., 1998. Palaeolithic society and the release from proximity: A network approach to intimate relations. *World Archaeol.* 29 (3), 426–449.
- García, N., Arsuaga, J.L., 2001. Les Carnivores (*Mammalia*) des sites du Pléistocène ancien et moyen d'Atapuerca (Espagne). *L'Anthropologie* 105, 83–93.
- García, N., Virgós, E., 2007. Evolution of community composition in several carnivore palaeoguilds from the European Pleistocene: The role of interspecific competition. *Lethaia* 40, 33–44.
- Gaudzinski, S., Roebroeks, W., 2001. Adults only. Reindeer hunter at the Middle Palaeolithic site Salzgitter-Lebenstedt, Northern Germany. *J. Hum. Evol.* 38, 497–521.
- Gaudzinski, S., Roebroeks, W., 2003. Profile analysis at Salzgitter-Lebenstedt. A reply to Munson and Marean. *J. Hum. Evol.* 44, 275–281.
- Gaudzinski, S., Niven, L., 2009. Hominin Subsistence Patterns during the Middle and Late Paleolithic in Northwestern Europe. In: Hublin, J.J., Richards, M.P. (Eds.), *The Evolution of Hominin Diets*. Springer, Leipzig, pp. 99–111.
- Gaudzinski, S., Turner, E., Anzidei, A.P., Álvarez-Fernández, E., Arroyo-Cabrales, J., Cinq-Mars, J., Dobosi, V.T., Hannus, A., Johnson, E., Münzel, S.C., Scheer, A., Villa, P., 2005. The use of Proboscidean remains in every-day Palaeolithic life. *Quat. Int.* 126–128, 179–194.
- Gaudzinski-Windheuser, S., 2006. Monospecific or species-dominated faunal assemblages during the Middle Paleolithic in Europe. In: Hovers, E., Kuhn, S.L. (Eds.), *Transitions before the Transition*. Springer, New York, pp. 137–147.
- Gaudzinski-Windheuser, S., 2021. Recapitulating Zooarchaeology at Salzgitter-Lebenstedt: Current State of Research and Perspectives. In: Gaudzinski-Windheuser, S., Jöris, O. (Eds.), *The Beef behind all Possible Past: The Tandem Festschrift in Honour of Elaine Turner and Martin Street*. Monographien des RGZM, Mainz, pp. 137–172.
- Gaudzinski-Windheuser, S., Kindler, L., 2012. Research perspectives for the study of Neanderthal subsistence strategies based on the analysis of archaeozoological assemblages. *Quat. Int.* 247, 59–68.
- Gaudzinski-Windheuser, S., Noack, E.S., Pop, E., Herbst, C., Pflöging, J., Buchli, J., Jacob, A., Enzmann, F., Kindler, L., Iovita, R., Street, M., Roebroeks, W., 2018. Evidence for close-range hunting by last interglacial Neanderthals. *Nat. Ecol. Evol.* 2, 1087–1092.
- Geraads, D., 1995. Carnívoros musterienses de la Cueva de Zafarraya (Málaga). *Cuaternario y geomorfología: revista de la Sociedad Española de Geomorfología y Asociación Española para el Estudio del Cuaternario*, 9 (3–4), 51–57.
- Germonpré, M., Hämäläinen, R., 2007. Fossil Bear Bones in the Belgian Upper Paleolithic: The Possibility of a Proto Bear-Ceremonialism. *Arctic Anthropology* 44 (2), 1–30.
- Germonpré, M., Udrescu, M., Fiers, E., 2013. The fossil mammals of Spy. In: Rougier, H., Semal, P. (Eds.), *Jemy Cave. 125 Years of Multidisciplinary Research at the Betche Aux Rotches (Jemeppe-Sur-Sambre, Province of Namur, Belgium)*. Société Royale Belge d'Anthropologie et de Préhistoire, Brussels, pp. 289–327.
- Goodman, N., 1978. *Ways of Worldmaking*. Hackett Publishing, Indianapolis.
- Gómez-Olivencia, A., Sala, N., Núñez-Lahuerta, C., Sanchis, A., Arlegi, M., Rios-Garzaiz, J., 2018. First data of Neanderthal bird and carnivore exploitation in the Cantabrian Region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Sci. Rep.* 8 (1), 10551.
- González-Ruibal, A., Hernando, A., Politis, G., 2011. Ontology of the self and material culture: Arrow-making among the Awá hunter-gatherers (Brazil). *J. Anthropol. Archaeol.* 30 (1), 1–16.
- Grubb, T.G., Lopez, R.G., Ellis, M.M., 2018. Winter Scavenging of Ungulate Carrion by Bald Eagles, Common Ravens, and Coyotes in Northern Arizona. *J. Raptor Res.* 52 (4), 471–483.
- Grusin, R. (Ed.), 2015. *The Nonhuman Turn*. University of Minnesota Press, Minneapolis.
- Grünberg, J.M., 2006. New AMS Dates for Palaeolithic and Mesolithic Camp Sites and Single Finds in Saxony-Anhalt and Thuringia (Germany). *Proc. Prehist. Soc.* 72, 95–112.
- Hahn, J. 1986. *Kraft und Aggression. Die Botschaft der Eiszeitkunst im Aurignacien Süddeuschlands?* Archaeologica Venatoria, Tübingen.
- Hajdinjak, M., Fu, Q., Hübner, A., Petr, M., Mafessoni, F., Grote, S., Skoglund, P., Narasimham, V., Rougier, H., Crevecoeur, I., Semal, P., Soressi, M., Talamo, S., Hublin, J.-J., Gušić, I., Kučan, Z., Rudan, P., Golovanova, L.V., Doronichev, V.B., Posth, C., Krause, J., Korlević, P., Nagel, S., Nickel, B., Slatkin, M., Patterson, N., Reich, D., Prüfer, K., Meyer, M., Pääbo, S., Kelso, J., 2018. Reconstructing the genetic history of late Neanderthals. *Nature* 555, 652–656.
- Hajdinjak, M., Mafessoni, F., Skov, L., Vernot, B., Hübner, A., Fu, Q., Essel, E., Nagel, S., Nickel, B., Richter, J., Moldovan, O.T., Constantin, S., Endarova, E., Zahariev, N., Spasov, R., Welker, F., Smith, G.M., Sinet-Mathiot, V., Paskulin, L., Fewlass, H., Talamo, S., Rezek, Z., Sirakova, S., Sirakov, N., McPherron, S.P., Tsanova, T., Hublin, J.-J., Peter, B.M., Meyer, M., Skoglund, P., Kelso, J., Pääbo, S., 2021. Initial Upper Palaeolithic humans in Europe had recent Neanderthal ancestry. *Nature* 592, 253–257. <https://doi.org/10.1038/s41586-021-03335-3>.
- Hallett, E.Y., Marean, C.W., Steele, T.E., Álvarez-Fernández, E., Jacobs, Z., Cerasoni, J.N., Aldeias, V., Scerri, E.M., Olszewski, D.I., El Hajraoui, M.A., Dibble, H.L., 2021. A worked bone assemblage from 120,000–90,000 year old deposits at Contrebandiers Cave, Atlantic Coast, Morocco. *Isceance* 24 (9), 102988.
- Haraway, D.J., 1991. *Simians, Cyborgs, and Women*. Free Association Books, London, The Reinvention of Nature.
- Haraway, D.J., 2003. *The Companion Species Manifesto: Dogs, People and Significant Otherness*. The University of Chicago Press, Chicago.
- Haraway, D.J., 2007. *When Species Meet*. University of Minnesota Press, Minneapolis.
- Haraway, D.J., 2016. *Staying with the Trouble: Making Kin in the Chthulucene*. Duke University Press, Durham.
- Hardy, B.L., Moncel, M.-H., 2011. Neanderthal use of fish, mammals, birds, starchy plants and wood 125–250,000 years ago. *PLoS ONE* 6 (8), e23768.
- Hardy, K., Buckley, S., Collins, M.J., Estalrich, A., Brothwell, D., Copeland, L., García-Taberner, A., García-Vargas, S., de la Rasilla, M., Lalueza-Fox, C., Huguet, R., Bastir, M., Santamaria, D., Madella, M., Wilson, J., Fernández-Cortés, A., Rosas, A., 2012. Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in dental calculus. *Naturwissenschaften* 99, 617–626.
- Harris, M., 1985. *Good to eat: riddles of food and culture*. Waveland, London.
- Harrison-Buck, E., Hendon, J.A. (Eds.), 2018. *Relational Identities and Other-Than-Human Agency in Archaeology*. University of Colorado Press, Boulder.
- Hastrup, K., 2014. *Anthropology and Nature*. Routledge, London.
- Hawkes, C., 1954. Archaeological theory and method: some suggestions from the old world. *Am. Anthropol.* 56 (2), 155–168.
- Hayden, B., 2012. Neanderthal social structure? *Oxford J. Archaeol.* 31 (1), 1–26.
- Haynes, G., 2006. Mammoth landscapes: good country for hunter-gatherers. *Quat. Int.* 142, 20–29.
- Hedges, R.E.M., Pettitt, P.B., Ramsey, C.B., Klinken, G.J.V., 1998. Radiocarbon Dates from the Oxford AMS System: Archaeometry Datelist 25. *Archaeometry* 40, 227–239.
- Henshilwood, C., d'Errico, F. (Eds.), 2011. *Homo symbolicus. The dawn of language, imagination and spirituality*. John Benjamins Publishing, Philadelphia/Amsterdam.
- Henson, L.H., Balkenhol, N., Gustas, R., Adams, M., Walkus, J., Housty, W.G., Stronen, A. V., Moody, J., Service, C., Reece, D., vonHoldt, B.M., McKechnie, I., Koop, B.F., Darimont, C.T., 2021. Convergent geographic patterns between grizzly bear population genetic structure and Indigenous language groups in coastal British Columbia, Canada. *Ecology and Society* 26 (3), 7. <https://doi.org/10.5751/ES-12443-260307>.
- Hertel, F., 1994. Diversity in body size and feeding morphology within past and present vulture assemblages. *Ecology* 75, 1074–1084.
- Herva, V.-P., Lahelma, A., 2020. *Northern Archaeology and Cosmology: A Relational View*. Routledge, London.
- Higham, T.F.G., Bronk Ramsey, C., Brock, F., Baker, D., Ditchfield, P., 2007. Radiocarbon dates from the oxford AMS system: archaeometry datelist 32. *Archaeometry* 49, 1–60.
- Hill, E., 2000. The contextual analysis of animal interments and ritual practice in southwestern North America. *Kiva* 65 (4), 361–398.
- Hill, E., 2012. The nonepiphrical past: Enculturated landscapes and other-than-human persons in Southwest Alaska. *Arctic Anthropol.* 49 (2), 41–57.
- Hill, E., 2013. *Archaeology and Animal Persons*. *Environ. Soc. ety* 4 (1), 117–136.
- Hill, E., 2019. *Humans, Birds and Burial Practices at Ipiutak, Alaska: Perspectivism in the Western Arctic*. *Environ. Archaeol.* 24 (4), 434–448.
- Hjorungdal, T., 2019. Reaching them a Human Paw: Relational Approaches to Ungulate Companions. *Archaeol. Rev. Cambridge* 34, 65–79.
- Hoffecker, J.F., 2017. *Modern Humans*. Columbia University Press, New York, Their Origin and Global Dispersal.
- Hoffecker, J.F., Cleghorn, N., 2000. Mousterian hunting patterns in the Northwestern Caucasus and the ecology of the neanderthals. *Int. J. Osteoarchaeol.* 10, 368–378.

- Holekamp, K.E., Smith, J.E., Strelloff, C.C., Van Horn, R.C., Watts, H.E., 2012. Society, demography and genetic structure in the spotted hyena. *Mol. Ecol.* 21, 613–632.
- Hollingshead, A.B., 1940. Human ecology and human society. *Ecol. Monogr.* 10 (3), 354–366.
- Hublin, J.J., Sirakov, N., Aldeias, V., Bailey, S., Bard, E., Delvigne, V., Endarova, E., Fagault, Y., Fewlass, H., Hajdinjak, H., Kromer, B., Krumov, I., Marreiros, J., Naomí, N.L., Martisius, L., Paskulin, L., Sinet-Mathiot, V., Meyer, M., Pääbo, S., Popov, V., Rezek, Z., Sirakova, S., Skinner, M.M., Smith, G.M., Spasov, R., Talamo, S., Tuna, T., Wacker, L., Welker, F., Wilcke, A., Zahariev, N., McPherron, S. P., Tsanova, S., 2020. Initial Upper Palaeolithic Homo sapiens from Bacho Kiro Cave, Bulgaria. *Nature* 581, 299–305.
- Huguet, R., Arsuaga, J.L., Pérez-González, A., Arriaza, M.C., Sala, N., Laplana, C., Sevilla, P., García, N., Álvarez-Lao, D., Blain, H.A., Baquedano, E., 2010. Homínidos y hienas en el Calvero de la Higuera (Pinilla del Valle, Madrid) durante el Pleistoceno Superior. Resultados preliminares. *Zona Arqueológica* 13, 444–458.
- Hussain, S.T., 2013. Homo empathicus – Versuch einer Evolutionären Anthropologie der Empathie. Implikationen für die anthropologische Bestimmung des modernen Menschen und das Verschwinden der letzten Neandertaler. Habelt, Bonn.
- Hussain, S.T., 2019. Gazing at Owls? Human-strigiform Interfaces and their Role in the Construction of Gravettian Lifeworlds in East-Central Europe. *Environ. Archaeol.* 24 (4), 359–376.
- Hussain, S.T. in press. Deep Animal Prehistory. Gathering Feral Voices from Vanished Pleistocene Worlds. In: Kitagawa, K., Diaz-Zorita, M., Tumolo, V. (Eds.), *Beyond Subsistence: New Approaches to Human-Animal Relations in the Past*. CRC 1070 Monographs, Tübingen.
- Hussain, S.T., Floss, H., 2015. Sharing the world with mammoths, cave lions and other beings: linking animal-human interactions and the Aurignacian “belief world”. *Quartär* 62, 85–120.
- Hussain, S.T., Breyer, T., 2017. Menschwerdung, Verkörperung und Empathie. Perspektiven im Schnittfeld von Anthropologie und Paläolitharchäologie. In: Eitzelmüller, G., Fuchs, T., Tewes, C. (Eds.), *Verkörperung – Eine neue interdisziplinäre Anthropologie*. De Gruyter, Berlin, pp. 211–250.
- Hussain, S.T., Will, M., 2021. The integrative potential of materiality theory in palaeolithic archaeology: lithic technology revisited. *J. Archaeol. Method Theory* 28 (2), 617–670.
- Hülle, W., 1977. Die Isenhöhle unter Burg Ranis/Thüringen. Gustav Fischer Verlag, Stuttgart/New York, Eine paläolithische Jägerstation.
- Iannucci, A., Mecozzi, B., Sardella, F., Iurino, D.A., 2021. The extinction of the giant hyena *Pachycrocuta brevirostris* and a reappraisal of the Epivillafranchian and Galerian Hyaenidae in Europe: Faunal turnover during the Early-Middle Pleistocene Transition. *Quat. Sci. Rev.* 272, 107240.
- Ilany, A., Holekamp, K.E., Akçay, E., 2021. Rank-dependent social inheritance determines social network structure in spotted hyenas. *Science* 373, 348–352.
- Ingold, T., 2000. *The Perception of the Environment: Essays in Livelihood, Dwelling, and Skill*. Routledge, New York.
- Ingold, T., 2013. *Making*. London, Routledge, Anthropology, Archaeology, Art and Architecture.
- Iovita, R., 2014. The role of edge angle maintenance in explaining technological variation in the production of Late Middle Paleolithic bifacial and unifacial tools. *Quat. Int.* 350, 105–115.
- Isaacs, J.R., Otruba, A., 2019. Guest Introduction: More-than-human contact zones. *ENE: Nat. Space* 2 (4), 697–711.
- Jacobi, R.M., Hawkes, C.J., 1993. Archaeological notes: work at the hyena den, wokey hole. *Proc. Univ. Bristol Spelaeol. Soc.* 19, 369–371.
- Jacobi, R.M., Higham, T.F.G., Ramsey, C.B., 2006. AMS radiocarbon dating of Middle and Upper Palaeolithic bone in the British Isles: improved reliability using ultrafiltration. *J. Quat. Sci.* 21, 557–573.
- Jacobi, R., Debenham, N., Catt, J., 2007. A Collection of Early Upper Palaeolithic Artefacts from Beeding, near Pulborough, West Sussex, and the Context of Similar Finds from the British Isles. *Proc. Prehist. Soc.* 73, 229–326.
- Jaouen, K., Richards, M.P., Le Cabec, A., Welker, F., Rendu, W., Hublin, J.J., Soressi, M., Talamo, S., 2019. Exceptionally high  $\delta^{15}N$  values in collagen single amino acids confirm Neandertals as high-trophic level carnivores. *Proc. Natl. Acad. Sci. US* 116 (11), 4928–4933.
- Jaubert, J., 1993. Le gisement paléolithique moyen de Mauran (Haute-Garonne): techno-économie des industries lithiques. *Bulletin de la Société préhistorique française* 90 (5), 328–335.
- Jaubert, J., Bordes, J.-G., Discamps, E., Gravina, B., 2011. A new look at the end of the Middle Palaeolithic Sequence in Southwestern France. In: Derevianko, A.P., Shunkov, M.V. (Eds.), *Characteristic Features of the Middle to Upper Paleolithic transition in Eurasia*. Asian Palaeolithic Association, Tokyo, pp. 102–115.
- Jéquier, C.A., Peresani, M., Romandini, M., Delpiano, D., Joannes-Boyau, R., Lembo, G., Livraghi, A., Lopez-García, J.M., Obradovic, M., Nicosia, C., 2015. The de Nadale cave, a single layered Quina mousterian site in the north Italy. *Quartär* 62, 7–21.
- Jéquier, C.A., Romandini, M., Peresani, M., 2012. Les retouchoirs en matières dures animales: une comparaison entre Moustérien final et Uluzzien. *Comptes Rendus Palevol* 11 (4), 283–292.
- Jimenez, E.-L., 2017. Modalités d’occupation du territoire et relations humains-grands Carnivores durant le Pléistocène supérieur: approche archéozoologique, taphonomique et paléocécologique du Bassin mosan belge dans son contexte nord-ouest européen. University Libre de Bruxelles. Doctoral Dissertation.
- Jimenez, E.-L., Germonpré, M., Boudin, M., 2021. Newinsights into cave hyena ethology and the implications for territorial competition with hominins in Late Pleistocene north-west Europe: the case of Caverne Marie-Jeanne (Belgium). *J. Quat. Sci.* 1–19 <https://doi.org/10.1002/jqs.3404>.
- Joffroy, R., Mouton, C., Paris, R., 1959. La grotte de la Roche-aux-Chats à Bâlot (Côte-d’Or). *Bulletin de la Société préhistorique de France* 56 (3–4), 205–209.
- Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.
- Jordan, P., 2003. *Material Culture and Sacred Landscape: The Anthropology of the Siberian Khanty*. Altamira Press, Walnut Creek.
- Jöris, O., 2014. Early Palaeolithic Europe. In: Renfrew, C., Bahn, P. (Eds.), *The Cambridge World Prehistory* 3. Cambridge University Press, Cambridge, pp. 1703–1746.
- Julien, M., Karlin, C. (Eds.), 2014. *Le campement magdalénien du niveau IV20*. Société préhistorique française, Paris.
- Kalof, L., 2007. *Looking at Animals in Human History*. The University of Chicago Press, Chicago.
- Kalof, L. (Ed.), 2017. *The Oxford Handbook of Animal Studies*. Oxford University Press, Oxford.
- Kane, A., Jackson, A.L., Ogada, D.L., Monadjem, A., McNally, L., 2014. Vultures acquire information on carcass location from scavenging eagles. *Proc. Roy. Soc. B* 281, 20141072.
- Karavanić, I., 2004. The Middle Palaeolithic Settlement of Croatia. In: Conard, N.J. (Ed.), *Settlement Dynamics of the Middle Paleolithic and Middle Stone Age, Volume II*. Kerns, Tübingen, pp. 185–200.
- Karavanić, I., Miracle, P.T., Culiberg, M., Kurtanjek, D., Zupanić, J., Golubić, V., Paunović, M., Mauch Lenardić, J., Malez, V., Šošić, R., Janković, I., Smith, F.H., 2008. The Middle Paleolithic from Mujina Pećina, Dalmatia, Croatia. *J. Field Archaeol.* 33, 259–277.
- Kellert, S.R., Black, M., Rush, C.R., Bath, A.J., 1996. Human culture and large carnivore conservation in North America. *Conserv. Biol.* 10 (4), 977–990.
- Kindler, L., 2012. *Die Rolle von Raubtieren bei der Einnischung und Subsistenz Jungpleistozäner Neandertaler*. Verlag des Römisch-Germanischen Zentralmuseums, Mainz, Archäologie und Taphonomie der Mittelpaläolithischen Fauna aus der Balver Höhle (Westfalen).
- Kirksey, S.E., Helmreich, S., 2010. The emergence of multispecies ethnography. *Cult. Anthropol.* 25 (4), 545–576.
- Kissel, M., Fuentes, A., 2020. The ripples of modernity: How we can extend paleoanthropology with the extended evolutionary synthesis. *Evol. Anthropol.* 30, 84–98.
- Kitagawa, K., 2014. *Exploring hominins and animals in the Swabian Jura: Study of the Paleolithic fauna from Hohlenstein-Stadel*. University of Tübingen, Tübingen. Unpublished PhD Dissertation.
- Kitagawa, K., Krönneck, P., Conard, N.J., Münzel, S., 2012. Exploring Cave Use and Exploitation Among Cave Bears, Carnivores and Hominins in the Swabian Jura Germany. *J. Taphonomy* 10 (3–4), 439–461.
- Kohn, E., 2013. *How Forests Think: Toward an Anthropology Beyond the Human*. University of California Press, Berkeley.
- Kolen, J., 1999. Hominids without homes: on the nature of Middle Palaeolithic settlement in Europe. In: Roebroeks, W., Gamble, C. (Eds.), *The Middle Palaeolithic occupation of Europe*. Leiden University Press, Leiden, pp. 139–175.
- Kolowski, J.M., Holekamp, K.E., 2007. Effects of an open refuse pit on space use patterns of spotted hyenas. *Afr. J. Ecol.* 46, 341–349.
- Kost, C., Hussain, S.T., 2019. Archaeo-ornithology: towards an archaeology of human-bird interface. *Environ. Archaeol.* 24 (4), 337–358.
- Kot, M., Richter, J., 2012. Leafpoints or rather “leafknives”? A technological analysis of bifacially shaped artefacts from mauren. *Anthropologie* L/3, 361–375.
- Krajcarz, M.T., Krajcarz, M., Ginter, B., Goslar, T., Wojtal, P., 2018. Towards a Chronology of the Jerzmanowician - a New Series of Radiocarbon Dates from Nietoperzowa Cave (Poland). *Archaeometry* 60, 383–401.
- Kruuk, H., 2002. *Hunter and Hunted: Relationships Between Carnivores and People*. Cambridge University Press, Cambridge.
- Kuhn, B.F., 2011. *Hyaenids: Taphonomy and Implications for the Palaeoenvironment*. Cambridge Scholars Publishing, Cambridge.
- Kuhn, S.L., 2013. *Cultural Transmission, Institutional Continuity and the Persistence of the Mousterian*. In: Akazawa, T., Nishiaki, Y., Aoki, K. (Eds.), *Dynamics of Learning in Neanderthals and Modern Humans, Volume 1: Cultural Perspectives*. Springer, Tokio, pp. 105–113.
- Lamb, C.T., Ford, A.T., McLellan, B.N., Proctor, M.F., Mowat, G., Ciarniello, L., Nielsen, S.E., Boutin, S., 2020. The ecology of human-carnivore coexistence. *Proc. Natl. Acad. USA* 117 (30), 17876–17883.
- Lambertucci, S.A., Speziale, K.L., Rogers, T.E., Morales, J.M., 2009. How do roads affect the habitat use of an assemblage of scavenging raptors? *Biodivers. Conserv.* 18, 2063–2074.
- Langlais, M., 2020. *Une anthologie du Paléolithique récent-final en France meridionale (21–11 Ka cal BP)*. University of Bordeaux 1, Bordeaux. Unpublished Habilitation.
- Langley, M.C., 2013. *Storied landscapes makes us (Modern) Human: Landscape socialisation in the Palaeolithic and consequences for the archaeological record*. *J. Anthropol. Archaeol.* 32, 614–629.
- Laroulandie, V., Faivre, J.-P., Gerbe, M., Mourre, V., 2016. Who brought the bird remains to the Middle palaeolithic site of les Fioux (Southwestern, France)? Direct evidence of a complex taphonomic story. *Quat. Int.* 421, 116–133.
- Laroulandie, V., Morin, E., Soulier, M.-C., Castel, J.-C., 2020. Bird procurement by humans during the Middle and early Upper Paleolithic of Europe: New data for the Aurignacian of southwestern France. *Quat. Int.* 543, 16–24.
- Lawson, V., 2007. *Geographies of Care and Responsibility*. *Ann. Assoc. Am. Geogr.* 97 (1), 1–11.
- Leder, D., Herrmann, R., Hüls, M., Russo, G., Hoelzmann, P., Nielbock, R., Böhner, U., Lehmann, J., Meier, M., Schwab, A., Tröller-Reimer, A., Koddenberg, T., Terberger, T., 2021. A 51,000-year-old engraved bone reveals Neanderthals’

- capacity for symbolic behaviour. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-021-01537-6>.
- Lestel, D., 2006. Ethology and ethnology: the coming synthesis A general introduction. *Soc. Sci. Inform.* 45 (2), 147–153.
- Lestel, D., Hollis, T., 2013. Shared life: an introduction. *Soc. Sci. Inform.* 52 (2), 183–186.
- Lewis, J., 2014. BaYaka Pygmy multi-modal and mimetic communication traditions. In: Dor, D., Knight, C., Lewis, J. (Eds.), *The Social Origins of Language*. Oxford University Press, Oxford. <https://doi.org/10.1093/acprof:oso/9780199665327.001.0001>.
- Lewis, M.E., Werdelin, L., 2010. Carnivora Dispersal Out of Africa During the Early Pleistocene: Relevance for Hominins? In: Fleagle, J.G., Shea, J.J., Grine, F.E., Baden, A.L., Leakey, R.E. (Eds.), *Out of Africa I - The First Hominin Colonization of Eurasia*. Springer, Dordrecht, pp. 13–26.
- Liebe, K.T., 1876. Die Lindenthaler Hyänenhöhle und andere diluviale Knochenfunde in Ostthüringen. *Archiv für Anthropologie* 155–172.
- Livingston, J., Puar, J.K., 2011. Interspecies. *Social Text* 29 (1), 3–14.
- Liolios, D., 2006. In: *Towards a Definition of the Aurignacian*, pp. 37–52.
- Lloveras, L., Moreno-García, M., Nadal, J., Zilhão, J., 2011. Who brought in the rabbits? Taphonomical analysis of Mousterian and Solutrean leporid accumulations from Gruta do Caldeirão (Tomar, Portugal). *J. Archaeol. Sci.* 38, 2434–2449.
- Locht, J.L., Hérisson, D., Gouval, E., Cliquet, D., Huet, B., Coutard, S., Antoine, P., Féry, P., 2016. Timescales, space and culture during the Middle Palaeolithic in northwestern France. *Quat. Int.* 411, 129–148.
- Locke, P., 2014. Interspecies Intersections: Ethnoprimateology and Ethnoelephantology. Paper presented at The University of Otago's Archaeology and Anthropology Seminar Series, 2 May 2014, <http://hdl.handle.net/10092/14373> (last accessed 27.07.2021).
- Locke, P., Münster, U., 2015. *Multispecies Ethnography*. Oxford Bibliographies. <https://doi.org/10.1093/OBO/9780199766567-0130>.
- Lorblanchet, M., 1999. La naissance de l'art. *Genèse de l'art préhistorique dans le monde*, Errance, Paris.
- Lorblanchet, M., Bahn, P., 2017. *The First Artists. In Search of the World's Oldest Art*. Thames & Hudson, London.
- Lorimer, J., 2007. Nonhuman Charisma. *Environ. Plan. D: Soc. Space* 25 (5), 911–932.
- Lorimer, J., Hodgetts, T., Barua, M., 2019. Animals' atmospheres. *Prog. Hum. Geogr.* 43 (1), 26–45.
- Mafessoni, F., Prüfer, K., 2017. Better support for a small effective population size of Neandertals and a long shared history of Neandertals and Denisovans. *PNAS* 114, 16918.
- Maher, L., 2021. Landscapes of the Past: Creation of Persistent Places in Hunter-gatherer Landscapes of Southwest Asia and Japan. *Japanese J. Archaeol.* 8, 247–283.
- Majkić, A., Evans, S., Stepanchuk, V., Tsvetlykh, A., d'Errico, F., 2017. A decorated raven bone from the Zaskalnaya VI (Kolosovskaya) Neandertal site, Crimea. *PLoS ONE* 12 (3), e0173435.
- Majkić, A., d'Errico, F., Milošević, S., Mihailović, D., Dimitrijević, V., 2018. Sequential Incisions on a Cave Bear Bone from the Middle Paleolithic of Pešturina Cave, Serbia. *J. Archaeol. Method Theory* 25, 69–116.
- Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.-C., Terborgh, J.W., 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *PNAS* 113 (4), 838–846.
- Malinowski, B., 1922. *Argonauts of the Western Pacific: An Account of Native Enterprise and Adventure in the Archipelagoes of Melanesian New Guinea*. New York, E.P. Dutton.
- Malone, N., Ovenden, K., 2017. *Natureculture*. In: Fuentes, A. (Ed.), *The International Encyclopedia of Primatology*. Wiley, New York. <https://doi.org/10.1002/9781119179313.wbprim0135>.
- Mania, D., Toepfer, V., 1973. *Königsau: Gliederung*. Deutscher Verlag der Wissenschaften, Berlin, Oekologie und Mittelpaläolithische Funde der letzten Eiszeit.
- Mania, D., Thomae, M., Litt, T., Weber, T., 1990. Neumark – Gröbern. Deutscher Verlag der Wissenschaften, Berlin, Beiträge zur Jagd des mittelpaläolithischen Menschen.
- Marciszak, A., Lipiecki, G., 2020. The history of bears (Ursidae, Carnivora, Mammalia) from Silesia (southern Poland) and the neighbouring areas. *Geol. Quart.* 64 (4), 876–897.
- Marciszak, A., Schouwenburg, C., Lipiecki, G., Talamo, S., Shpansky, A., Malikov, D., Gornig, W., 2019. Steppe brown bear *Ursus arctos* "priscus" from the Late Pleistocene of Europe. *Quat. Int.* 534, 158–170.
- Marín, J., Saladié, P., Rodríguez-Hidalgo, A., Carbonell, E., 2017. Ungulate carcass transport strategies at the Middle Palaeolithic site of Abric Romaní (Capellades, Spain). *C.R. Palevol* 16, 103–121.
- Marín, J., Rodríguez-Hidalgo, A., Saladié, P., Boulbes, N., Magniez, P., Testu, A., Moigne, A.-M., 2020. Taphonomic analysis of horse remains from Mousterian and Aurignacian Units from Bize-Tournal Cave (Aude, France). *C.R. Palevol* 19 (11), 187–213.
- Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline: An appraisal of the human health and other benefits of vultures in India. *Ecol. Econ.* 67, 194–204.
- Marquet, J.-C., 1999. *La Préhistoire en Touraine*. Editions CLD, Chambray les Tours.
- Marshack, A., 1991. A reply to Davidson on Mania and Mania. *Rock Art Res.* 8, 47–58.
- Martin, D., 1996. On the Cultural Ecology of Sky Burial on the Himalayan Plateau. *East and West* 46 (3/4), 353–370.
- Martínez-Sánchez, R.M., López-García, J.M., Blain, H.-A., Rabal-Garcés, R., Bretones-García, M.D., Rodríguez-Vidal, J., Martínez-Aguirre, A., 2012. Bears and Hyenas from the Latest Pleistocene of Southern Iberia: Sima de Abraham. *Priego de Córdoba, Andalusia*.
- Martísius, N.L., Welker, F., Dogandžić, T., Grote, M.N., Rendu, W.R., Sinet-Mathiot, V., Wilcke, A., McPherron, S.J.P., Soressi, M., Steele, T.E., 2020. Non-destructive ZooMS identification reveals strategic bone tool raw material selection by Neandertals. *Sci. Rep.* 10 (1), 1–12.
- Maureille, B., Costamagno, S., Beauval, C., Mann, A.E., Garralda, M.D., Mussini, C., Laroulandie, V., Rendu, W., Royer, A., Seguin, G., Vandermeersch, B., 2017. The challenges of identifying partially digested human teeth: first description of Neandertal remains from the Mousterian site of Marillac (Marillac-le-Franc, Charente, France) and implications for palaeoanthropological research. *Paléo* 28, 201–212.
- Mauss, M., 1967. *The Gift: Forms and Functions of Exchange in Archaic Societies*. Norton, New York, W.W.
- Maynard, J., 2022. Yuraki – an Australian Aboriginal perspective on deep history. In: McGrath, A., Russell, L. (Eds.), *The Routledge Companion to Global Indigenous History*. Routledge, Oxon/New York, pp. 722–735.
- Mazo, C., Alcolea, M., 2020. New data concerning Neandertal occupation in the Iberian System: First results from the late Pleistocene (MIS 3) Aguilón P5 cave site (NE Iberia). *Quat. Int.* 551, 105–122.
- McBryde, I., 2000. Travellers in storied landscapes: a case study in exchanges and heritage. *Aboriginal History* 24, 152–174.
- Meillassoux, C., 1973. On the mode of production of the hunting band. In: Alexandre, P. (Ed.), *French perspectives in African studies*. Oxford University Press, London, pp. 187–203.
- Meinig, D.W., 1979. The Beholding Eye: Ten Versions of the Same Scene. In: Meinig, D. W. (Ed.), *The Interpretation of Ordinary Landscapes: Geographical Essays*. Oxford University Press, Oxford, pp. 33–48.
- Mellars, P., 1996. *The Neandertal Legacy*. Princeton University Press, Princeton (NJ), An Archaeological Perspective from Western Europe.
- Menninghaus, W., 2011. *Wozu Kunst? Ästhetik nach Darwin*, Suhrkamp, Berlin.
- Mhlanga, M., Ramesh, T., Rhidikka, K., Ngosi, E., Downs, T.C., 2017. Comparison of spotted hyena (*Crocuta crocuta*) prey in two protected wildlife land-use types, a hunting area and a nonhunting area, in western Zimbabwe. *Afr. J. Ecol.* 56, 675–678.
- Mithen, S., 1996. *The Prehistory of the Mind*. Thames & Hudson, London, A Search for the Origins of Art, Religion and Science.
- Mithen, S., 1999. The Hunter-Gatherer Prehistory of Human-Animal Interactions. *Antrozoös* 12 (4), 195–204.
- Mithen, S., 2006. *The Singing Neanderthals: The Origins of Music, Language, Mind, and Body*. Harvard University Press, Cambridge (MA).
- Mithen, S., 2013. The Cathedral Model for the Evolution of Human Cognition. In: Hatfield, G., Pittman, H. (Eds.), *Evolution of Mind, Brain, and Culture*. University of Pennsylvania Museum of Archaeology and Anthropology, Philadelphia, pp. 217–233.
- Miracle, P.T., 2005. Late Mousterian subsistence and cave use in Dalmatia: The zooarchaeology of Mujina Pećina, Croatia. *International Journal of Osteoarchaeology* 15, 84–105.
- Miracle, P.T., 2007. *The Krapina Paleolithic Site: Zooarchaeology. Taphonomy and Catalog of the Faunal Remains*, Croatian Natural History Museum, Zagreb.
- Miracle, P.T., Mauch Lenardić, J., Brajković, D., 2010. Last glacial climates, "Refugia", and faunal change in Southeastern Europe: Mammalian assemblages from Veternica, Velika pećina, and Vindija caves (Croatia). *Quat. Int.* 212, 137–148.
- Moléon, M., Sánchez-Zapata, J.A., Margalida, A., Carrete, M., Owen-Smith, N., Donazar, J.A., 2014. Humans and scavengers: the evolution of interactions and ecosystem services. *Bioscience* 64, 394–403.
- Moncel, M.H., Poulet, S., Daujeard, C., Lartigot-Campin, A.S., Millet, J.J., Theodoropoulou, A., Cregut-Bonnoure, E., Gély, B., Vercoutere, C., Desclaux, E., Roger, T., Bourges, F., 2012. La Grotte du Figuier (Saint-Martin-d'Ardèche): bilan des travaux récents sur un site du Paléolithique moyen et supérieur de la moyenne vallée du Rhône (Sud-Est de la France). *Bulletin de la Société préhistorique française* 109 (1), 35–67.
- Monsarrat, S., Kerley, G.I.H., 2018. Charismatic species of the past: Biases in reporting of large mammals in historical written sources. *Biol. Conserv.* 223, 68–75.
- Morin, E., Laroulandie, V., 2012. Presumed symbolic use of diurnal raptors by Neandertals. *PLoS ONE* 7 (3), e32856.
- Morin, E., Speth, J.D., Lee-Thorp, J., 2016. Middle Palaeolithic Diets: A Critical Examination of the Evidence. In: Lee-Thorp, J., Katzenberg, M.A. (Eds.), *The Oxford Handbook of the Archaeology of Diet*. Oxford Handbooks Online. <https://doi.org/10.1093/oxfordhb/9780199694013.013.24>.
- Morley, M.W., Goldberg, P., Uliyanov, V.A., Kozlikin, M.B., Shunkov, M.V., Derevianko, A.P., Jacobs, Z., Roberts, R.G., 2019. Hominin and animal activities in the microstratigraphic record from Denisova Cave (Altai Mountains, Russia). *Sci. Rep.* 9, 13785.
- Morphy, H., 1999. *Traditional and Modern Visual Art of Hunting and Gathering People*. In: Lee, R.B., Daly, R. (Eds.), *The Cambridge Encyclopedia of Hunters and Gatherers*. Cambridge University Press, Cambridge, pp. 441–448.
- Mouton, P., Joffroy, R., 1948. Paléolithique moyen et repère d'hyènes au « Perthis de Roche » de Morancourt (Haute-Marne). *Bulletin de la Société préhistorique de France* 45 (6–8), 256–259.
- Musharbash, Y., 2017. Telling Warlpiri Dog Stories. *Anthropol. Forum* 27 (7), 95–113.
- Mussi, M., 1988. Continuité et discontinuité dans les pratiques funéraires au Paléolithique: le cas de l'Italie. In: Otte, M. (Ed.), *L'Homme de Néandertal, Volume 5. Le Pensée*. ERAUL, Liège, pp. 93–107.
- Mussini, C., 2011. *Les restes humains mousteriens des Pradelles (Marillac-le-Franc, Charente, France) fouilles Maureille-Mann: étude morphométrique et réflexions sur un aspect comportemental des Néandertaliens*. University of Bordeaux I. Doctoral Dissertation.
- Müller-Beck, H.-J., 1968. A Possible Source for the Vogelherd Aurignacian. *Arctic Anthropol.* 5 (1), 48–61.

- Münzel, S.C., Conard, N.J., 2004. Cave bear hunting in Hohle Fels cave in the Ach valley of the Swabian Jura. *Rev. Paléobiol.* 23 (2), 877–885.
- Nadasdy, P., 2003. Hunters and Bureaucrats: Power, Knowledge, and Aboriginal-State Relations in the Southwest Yukon. UBC Press, Vancouver/Toronto.
- Nadasdy, P., 2007. The gift in the animal: the ontology of hunting and human-animal sociality. *Am. Ethnol.* 34 (1), 25–43.
- Naiman, R.J., 1988. How animals shape their ecosystems. *BioScience* 38 (11), 750–752.
- Nance, S. (Ed.), 2015. *The Historical Animal*. Syracuse University Press, New York.
- Negro, J.J., 2018. Raptors and People: An Ancient Relationship Persisting Today. In: Sarasola, J.H., Grande, J.M., Negro, J.J. (Eds.), *Birds of Prey. Biology and conservation in the XXI century*, Springer, Cham, pp. 161–176.
- Nikulina, A., MacDonald, K., Scherjon, F., Pearce, E.A., Davoli, M., Svenning, J.-C., Vella, E., Gaillard, M.-J., Zapolska, A., Arthur, F., Martinez, A., Hatlestad, K., Mazier, F., Serge, M.A., Lindholm, K.-J., Fyfe, R., Renssen, H., Roche, D.M., Kluiwing, S., Roebroeks, W., 2022. Tracking Hunter-Gatherer Impact on Vegetation in Last Interglacial and Holocene Europe: Proxies and Challenges. *J. Archaeol. Method Theory*. <https://doi.org/10.1007/s10816-021-09546-2>.
- Niven, L., Steele, T.E., Rendu, W., Mallye, J.-B., McPherron, S.P., Soressi, M., Jaubert, J., Hublin, J.J., 2012. Neanderthal mobility and large-game hunting: The exploitation of reindeer during the Quina Mousterian at Chez-Pinaud Jonzac (Charente-Maritime, France). *J. Hum. Evol.* 63 (4), 624–635.
- Norton-Smith, T., 2010. *The Dance of Person and Place: One Interpretation of American Indian Philosophy*. State University of New York Press, Albany.
- Nowell, A., 2013. Cognition, Behavioral Modernity, and the Archaeological Record of the Middle and Early Upper Paleolithic. In: Hatfield, G., Pittman, H. (Eds.), *Evolution of Mind, Brain, and Culture*. University of Pennsylvania Museum of Archaeology and Anthropology, Philadelphia, pp. 235–262.
- O'Connor, T., 2013. *Animals as Neighbors*. Michigan State University Press, East Lansing.
- Ogden, L.A., 2011. *Swamplife. People, Gators, and Mangroves Entangled in the Everglades*. University of Minnesota Press, Minneapolis/London.
- Ogden, L., Hall, B., Tanita, K., 2013. Animals, plants, people, and things: a review of multispecies ethnography. *Environ. Soc. Adv. Res.* 4 (1), 5–24.
- Orbach, M., Yeshurun, R., 2019. The hunters or the hunted: Human and hyena prey choice divergence in the Late Pleistocene Levant. *J. Hum. Evol.* 160, 102572.
- Orr, M.R., Nelson, J.D., Watson, J.W., 2019. Heterospecific information supports a foraging mutualism between corvids and raptors. *Anim. Behav.* 153, 105–113.
- Overton, N., Hamilakis, J., 2013. A manifesto for a social zooarchaeology. Swans and other beings in the Mesolithic. *Archaeol. Dial.* 20 (2), 111–136.
- Pacheco, F.G., Giles Guzmán, F.J., Gutiérrez López, J.M., Pérez, A.S., Finlayson, C., Rodríguez Vidal, J., Finlayson, G., Fa, D.A., 2012. The tools of the last Neanderthals: Morphotechnical characterisation of the lithic industry at level IV of Gorham's Cave, Gibraltar. *Quat. Int.* 247, 151–161.
- Pálsson, G., 1996. Human-environmental relations: orientalism, paternalism and communalism. In: Descola, P., Pálsson, G. (Eds.), *Nature and Society: Anthropological perspectives*. Routledge, London/New York, pp. 63–81.
- Parfitt, S.A., Barendregt, R.W., Breda, M., Candy, I., Collins, M.J., Coope, G.R., Durbidge, P., Field, M.H., Lee, J.R., Lister, A.M., Mutch, R., Penkman, K.E.H., Preece, R.C., Rose, J., Stringer, C.B., Symmons, R., Whittaker, J.E., Wymer, J.J., Stuart, A.J., 2005. The earliest record of human activity in northern Europe. *Nature* 438, 1008–1012.
- Pastors, A., 2001. Die mittelpaläolithische Freilandstation von Salzgitter-Lebenstedt: Genese der Fundstelle und Systematik der Steinbearbeitung. *Ruth Printmedien, Braunschweig*.
- Patou, M., 1988. Consommation Courante de l'Ours des Cavernes en Europe Occidentale durant le Paléolithique Moyen: Mythe et Réalité. *Anthropozoologica* 2, 17–20.
- Patou-Mathis, M., 2000. Neanderthal Subsistence Behaviours in Europe. *Int. J. Osteoarchaeol.* 10, 379–395.
- Pauret-Homerville, C., Argant, A., Combier, J., Gély, B., Argant, J., 2011. La Grotte aux Ours de Châteaubourg (Ardèche, France): synthèse sur un gisement découvert il y a un siècle et demi. *Quaternaire* 2011, 185–199.
- Peigné, S., Goillot, C., Geronpre, M., Blondel, C., Bignon, O., Merceron, G., 2009. Predomancy omnivory in European cave bears evidenced by a dental microwear analysis of *Ursus spelaeus* from Goyet, Belgium. *Proc. Natl. Acad. Sci.* 106, 15390–15393.
- Pelegrin, J., 2013. Les grandes feuilles de laurier et autres objets particuliers du Solutrén: une valeur de signe. In: *Société d'études et de recherche archéologiques sur le Paléolithique de la vallée de la Claise* (Ed.), *Le Solutrén, 40 ans après Smith '66*. R.A.C.F., Tours, pp. 143–164.
- Peresani, M., 2012. Fifty thousand years of flint knapping and tool shaping across the Mousterian and Uluzzian sequence of Fumane cave. *Quat. Int.* 247, 125–150.
- Peresani, M., Fiore, I., Gala, M., Romandini, M., Tagliacozzo, A., 2011. Late Neanderthals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy. *Proceedings of the National Academy of Sciences of the United States of America* 108 (10), 3888–3893.
- Peresani, M., Vanhaeren, M., Quaggiotto, E., Queffelec, A., d'Errico, F., 2013. An ochered fossil marine shell from the Mousterian of Fumane Cave, Italy. *PLoS ONE* 8 (7), e68572.
- Peresani, M., Dellatorre, S., Astuti, P., Dal Colle, M., Ziggioni, S., Peretto, C., 2014. Symbolic or utilitarian? Juggling interpretations of Neanderthal behavior: new inferences from the study of engraved stone surfaces. *J. Anthropol. Sci.* 92, 233–255.
- Peterson, N., 1993. Demand sharing: reciprocity and the pressure for generosity among foragers. *Am. Anthropol.* 95 (4), 860–874.
- Pettitt, P., 2002. The Neanderthal dead: exploring mortuary variability in Middle Paleolithic Eurasia. *Before Farming* 1 (4), 1–19.
- Pettitt, P., 2011. *The Palaeolithic Origins of Human Burial*. Routledge, London.
- Pettitt, P., 2015. Landscapes of the Dead: The evolution of human mortuary activity from body to place in Palaeolithic Europe. In: Coward, F., Hosfield, R., Pope, M., Wenban-Smith, F. (Eds.), *Settlement, Society and Cognition in Human Evolution: Landscapes in Mind*. Cambridge University Press, Cambridge, pp. 258–274.
- Pettitt, P., 2018. Hominin evolutionary thanatology from the mortuary to funerary realm: the palaeoanthropological bridge between chemistry and culture. *Philos. Trans. Roy. Soc. Lond. B* 373, 20180212.
- Pettitt, P., White, M., 2012. *The British Palaeolithic. Human Societies at the Edge of the Pleistocene World*, Routledge, London.
- Picin, A., 2016. Short-term occupations at the lakeshore: a technological reassessment of the open-air site Königsau (Germany). *Quartär* 63, 7–32.
- Picin, A., Blasco, R., Arilla, M., Rivals, F., Chacón, G., de Soler, B., Talamo, S., Rosell, J., 2020. Short-Term Neanderthal Occupations and Carnivores in the Northeast of Iberian Peninsula. In: Cascalheira, J., Picin, A. (Eds.), *Short-Term Occupations in Paleolithic Archaeology. Definition and Interpretation*, Springer, Cham, pp. 183–213.
- Pierotti, R., Fogg, B.R., 2017. *The Coevolution of Wolves and Humans. How Wolves and Humans Coevolved*. Yale University Press, Yale, The First Domestication.
- Pilaar Birch, S. (Ed.), 2018a. *Multispecies Archaeology*. Routledge, London.
- Pilaar Birch, S., 2018b. Introduction. In: Pilaar Birch, S. (Ed.), *Multispecies Archaeology*. Routledge, London, pp. 1–7.
- Plumet, P., 2006. L'homme préhistorique dans le Grand Nord. *Compte Rendu Palevol* 5, 329–342.
- Politis, G.G., 1996. Moving to produce: Nukak mobility and settlement patterns in Amazonia. *World Archaeology* 27 (3), 492–511.
- Potter, E., Hawkins, G., 2009. *Naturecultures: Introduction*. Australian Humanities Review 46 (1), 39–41.
- Poole, K., 2015. The Contextual Cat: Human-Animal Relations and Social Meaning in Anglo-Saxon England. *Journal of Archaeological Method and Theory* 22, 857–882.
- Porr, M., 2015. Beyond Animality and Humanity. Landscape, Metaphor and Identity in the Early Upper Paleolithic of Central Europe. In: Coward, F., Hosfield, R., Pope, M., Wenban-Smith, F. (Eds.), *Settlement, Society and Cognition in Human Evolution: Landscapes in Mind*. Cambridge University Press, New York, pp. 54–74.
- Porr, M., Matthews, J.M., 2017. Post-Colonialism, Human Origins and the Paradox of Modernity. *Antiquity* 91 (358), 1058–1068.
- Pratt, M.L., 1991. Arts of the contact zone. *Profession* 33–40.
- Pratt, M.L., 2008. *Imperial Eyes: Travel Writing and Transculturation*, 2nd ed. Routledge, New York.
- Price, J., 1975. Sharing: the integration of intimate economies. *Anthropologia* 17, 3–27.
- Priestley, E., 2020. Beating the Dead Horse? Using Ethnography for Middle Paleolithic Zooarchaeological Contexts in North-West Europe. In: Kaercher, K., Arntz, M., Bomentre, N., Hermoso-Buxán, X.L., Kay, K., Ki, S., Macleod, R., Muñoz-Mojado, H., Timbrell, L., Wisher, I. (Eds.), *New Frontiers in Archaeology*. Archaeopress, Oxford, pp. 136–152.
- Prüfer, K., Posth, C., Yu, H., Stössel, A., Spyrou, M.A., Deviese, T., Mattoni, M., Ribechini, E., Higham, T., Velemínský, P., Brůžek, J., Krause, J., 2021. A genome sequence from a modern human skull over 45,000 years old from Zlatý kůň in Czechia. *Nat. Ecol. Evol.* 5, 820–825. <https://doi.org/10.1038/s41559-021-01443-x>.
- Qu, F., 2017. Ivory versus Antler: A Reassessment of Binary Structuralism in the Study of Prehistoric Eskimo Cultures. *Arctic Anthropol.* 54 (1), 90–109.
- Radović, D., Sršen, A.O., Radović, J., Frayer, D.W., 2015. Evidence for Neanderthal jewelry: modified white-tailed eagle claws at Krapina. *PLoS One* 10 (3), e0119802.
- Ravnsbæk Holm, S., Svenning, J.-C., 2014. 180,000 Years of Climate Change in Europe: Avifaunal Responses and Vegetation Implications. *PLoS ONE* 9 (4), e94021. <https://doi.org/10.1371/journal.pone.0094021>.
- Rendu, W., Costamagno, S., Meignen, L., Soulier, M.-C., 2012. Monospecific faunal spectra in Mousterian contexts: Implications for social behavior. *Quat. Int.* 247, 50–58.
- Rendu, W., Beauval, C., Crevecoeur, I., Bayle, P., Balzeau, A., Bismuth, T., Bourguignon, L., Delfour, G., Faivre, J.-P., Lacrampe-Cuyaubère, F., Tavormina, C., Todisco, D., Turq, A., Maureille, B., 2014. Evidence supporting an intentional Neanderthal burial at La Chapelle-aux-Saints. *PNAS* 111, 81–86.
- Rendu, W., Beauval, C., Crevecoeur, I., Bayle, P., Balzeau, A., Bismuth, T., Bourguignon, L., Delfour, G., Faivre, J.-P., Lacrampe-Cuyaubère, F., Muth, X., Pasty, S., Semal, P., Tavormina, C., Todisco, D., Turq, A., Maureille, B., 2016. Let the dead speak... comments on Dibble et al.'s reply to "Evidence supporting an intentional burial at La Chapelle-aux-Saints". *J. Archaeol. Sci.* 69, 12–20.
- Rendu, W., Renou, S., Soulier, M.-C., Rigaud, S., Roussel, M., Soressi, M., 2019. Subsistence strategy changes during the Middle to Upper Paleolithic transition reveals specific adaptations of Human Populations to their environment. *Sci. Rep.* 9, 15817.
- Richards, M.P., Pettitt, P.B., Trinkaus, E., Smith, F.H., Paunović, M., Karavanić, I., 2000. Neanderthal diet at Vindija and Neanderthal predation: the evidence from stable isotopes. *PNAS* 97 (13), 7663–7666.
- Richter, J., 2018. *Altsteinzeit. Der Weg des frühen Menschen von Afrika bis in die Mitte Europas*. Kohlhammer, Cologne.
- Riek, G., 1938. Ein Beitrag zur Kenntnis des süddeutschen Solutrén. *Germania* 22 (3), 147–150.
- Rios-Garaizar, J., 2010. Organización económica de las sociedades neandertales: El caso del nivel vii de amalda (zestoa, gipuzkoa) Economic organization among Neanderthals: Amalda (Basque Country, Spain) level VII Mousterian. *Zephyrus* 65, 15–37.
- Rios-Garaizar, J., Arrizabalaga, A., Villaluenga, A., 2012. Haltes de chasse du Châtelperonnien de la Péninsule Ibérique: Labeko Koba et Ekain (Pays Basque Péninsulaire). *L'anthropologie* 116, 532–549.

- Renfrew, C., Morley, I. (Eds.), 2009. *Becoming Human. Innovation in Prehistoric Material and Spiritual Culture*. Cambridge University Press, Cambridge.
- Richter, J., 2009. The role of leaf points in the Late Middle Palaeolithic of Germany. *Præhistoria* 9–10, 99–113.
- Ritvo, H., 2007. On the animal turn. *Daedalus* 136 (4), 118–122.
- Rival, L., 2012. The materiality of life: Revisiting the anthropology of nature in Amazonia. *Indiana* 29, 127–143.
- Rockman, M., 2013. Apprentice to the environment: hunter-gatherers and landscape learning. In: Wendrich, W. (Ed.), *Archaeology and apprenticeship: body knowledge, identity, and communities of practice*. University of Arizona Press, Tucson, pp. 99–118.
- Rodríguez-Hidalgo, A., 2010. The scavenger or the scavenged? *Journal of Taphonomy* 8, 75–76.
- Rodríguez-Hidalgo, A., Morales, J.I., Cebria, A., Courtenay, L.A., Fernández-Marchena, J. L., García-Argudo, G., Marín, J., Saladié, P., Soto, M., Tejero, J.-M., Fullola, J.-M., 2019. The Châtelperronian Neanderthals of Cova Foradada (Calafell, Spain) used imperial eagle phalanges for symbolic purposes. *Science Advances* 5, eaax1984.
- Roebroeks, W., Soressi, M., 2016. Neandertals revised. *Proc. Natl. Acad. Sci. United States* 113 (23), 6372–6379.
- Roebroeks, W., MacDonald, K., Scherjon, F., Bakels, C., Kindler, L., Nikulina, A., Pop, E., Gaudzinski-Windheuser, S., 2021. Landscape modification by Last Interglacial Neanderthals. *Sci. Adv.* 7, eabj5567.
- Rohland, N., Pollack, J.L., Nagel, D., Beauval, C., Airvaux, J., Pääbo, S., Hofreiter, M., 2005. The population history of extant and extinct hyenas. *Mol. Biol. Evol.* 22 (12), 2435–2443.
- Romandini, M., Peresani, M., Laroulandie, V., Metz, L., Pastroors, A., Vaquero, M., Slimak, L., 2014. Convergent evidence of eagle talons used by late Neanderthals in Europe: a further assessment on symbolism. *PLoS ONE* 9 (7), e101278.
- Romandini, M., Fiore, I., Gala, M., Cestari, M., Guida, G., Tagliacozzo, A., Peresani, M., 2016. Neanderthal scraping and manual handling of raptors wing bones: evidence from Fumane Cave. *Experimental activities and comparison*. *Quat. Int.* 421, 154–172.
- Romandini, M., Terlato, G., Nannini, N., Tagliacozzo, A., Benazzi, S., Peresani, M., 2018. Bears and humans, a Neanderthal tale. Reconstructing uncommon behaviors from zooarchaeological evidence in southern Europe. *J. Archaeol. Sci.* 90, 71–91.
- Rougier, H., Crevecoeur, I., Beauval, C., Posth, C., Flas, D., Wißing, C., Furtwängler, A., Germonpré, M., Gómez-Olivencia, A., Semal, P., Van der Plicht, J., 2016. Neanderthal cannibalism and Neanderthal bones used as tools in Northern Europe. *Sci. Rep.* 6 (1), 1–11.
- Ruebens, K., 2013. Regional behaviour among late Neanderthal groups in Western Europe: a comparative assessment of late Middle Palaeolithic bifacial tool variability. *J. Hum. Evol.* 65 (4), 341–362.
- Rusch, L., Grégoire, S., Pois, V., Moigne, A.M., 2019. Neanderthal and carnivore occupations in unit II from the Upper Pleistocene site of Ramandils Cave. *J. Archaeol. Sci.: Rep.* 28, 102038.
- Rutherford, S., Wilcox, S., 2018. A meeting place. In: Wilcox, S., Rutherford, S. (Eds.), *Historical Animal Geographies*. Routledge, London/New York, pp. 3–9.
- Sala, N., Algaba, M., Arsuaga, J.L., Aranburu, A., Pantoja, A., 2012. A taphonomic study of the Búho and Zarzamora caves. Hyenas and humans in the Iberian Plateau (Segovia, Spain) during the Late Pleistocene. *J. Taphonomy* 10, 477–497.
- Sala, N., Pablos, A., Gómez-Olivencia, A., Sanz, A., Villalba, M., Pantoja-Pérez, A., Laplana, C., Luis Arsuaga, J., Algaba, M., 2020. Central Iberia in the middle MIS 3. Paleoeological inferences during the period 34–40 cal kyr BP. *Quat. Sci. Rev.* 228, 106027.
- Sanchis, A., Tormo, C., Sauqué, V., Sanchis, V., Díaz, R., Ribera, A., Villaverde, V., 2015. Pleistocene leopards in the Iberian Peninsula: new evidence from palaeontological and archaeological contexts in the Mediterranean region. *Quat. Sci. Rev.* 124, 175–208.
- Sanchis, A., Real, C., Sauqué, V., Núñez-Lahuerta, C., Éguez, N., Tormo, C., Pérez Ripoll, M., Carrión Marco, Y., Duarte, E., 2019. Neanderthal and carnivore activities at Llonin Cave, Asturias, northern Iberian Peninsula: faunal study of Mousterian levels (MIS 3). *C.R. Palevol* 18 (1), 113–141.
- Sanz, M., Daura, J., Éguez, N., Cabanes, D., 2017. On the track of anthropogenic activity in carnivore dens: altered combustion structures in Cova del Gegant (NE Iberian Peninsula). *Quat. Int.* 437, 102–114.
- Sartwell, C., 2009. *Aesthetics of the Everyday*. In: Levinson, J. (Eds.), *The Oxford Handbook of Aesthetics* (online). Oxford University Press, New York, 10.1093/oxfordhb/9780199279456.003.0046.Sax, B., 2001. *The Mythical Zoo: An Encyclopedia of Animals in World Myths, Legend, and Literature*. ABC-CLIO, Santa Barbara et al.
- Sauqué, V., Galán, J., Núñez-Lahuerta, C., Sola-Almagro, C., Rabal-Garcés, R., Martínez, I., Mazo, C., Cuenca-Bescós, G., 2014. Neandertales en el Pleistoceno Superior del valle del Ebro, paeloambiente y evidencias tafonómicas en Aguilón P-7. *Jornadas de Paleontología de la Sociedad Española de Paleontología Fundamental* 24, 223–226.
- Sauqué, V., Rabal-Garcés, R., Madurell-Malaperia, J., Gisbert, M., Zamora, S., de Torres, T., Ortiz, J.E., Cuenca-Bescós, G., 2017. Pleistocene cave hyenas in the Iberian Peninsula: New insights from Los Aprendices cave (Moncayo, Zaragoza). *Palaeontol. Electronica* 20 (1/11A), 1–38.
- Sax, B., 2001. *The Mythical Zoo. An Encyclopedia of Animals in World Myth, Legend, and Literature*. ABC-CLIO, Santa Barbara et al.
- Schütz, A., 1993. *Der sinnhafte Aufbau der sozialen Welt: Eine Einleitung in die verstehende Soziologie*. Main, Suhrkamp, Frankfurt a.
- Selvaggio, M.M., 1994. Carnivore tooth marks and stone tool butchery marks on scavenged bones: archaeological implications. *J. Hum. Evol.* 27, 215–228.
- Semal, P., Hauzeur, A., Rougier, H., Crevecoeur, I., Germonpré, M., Pirson, S., Haesaerts, P., Jungels, C., Flas, D., Toussaint, M., Maureille, B., Bocherens, H., Higham, T., van der Plicht, J., 2013. Radiocarbon dating of human remains and associated archaeological material. In: Rougier, H., Semal, P. (Eds.), *Spy Cave. 125 Years of Multidisciplinary Research at the Betche Aux Rotches (Jemeppe-Sur-Sambre, Province of Namur, Belgium)*, *Anthropologica et Præhistorica* 123/2012. Société Royale Belge d'Anthropologie et de Préhistoire, Brussels, pp. 331–356.
- Serangeli, J., Bolus, M., 2008. Out of Europe – The dispersal of a successful European hominin form. *Quartär* 55, 83–98.
- Serpell, J., 1989. Pet-keeping and animal domestication: a reappraisal. In: Clutton-Brock, J. (Ed.), *The walking larder: patterns of domestication, pastoralism, and predation*. Unwin Hyman, London, pp. 10–21.
- Shaw, A., Bates, M., Conneller, C., Gamble, C., Julien, M.-A., McNabb, J., Pope, M., Scott, B., 2016. The Archaeology of Persistent Places: The Palaeolithic Case of La Cotte de St Brelade, Jersey. *Antiquity* 90, 1437–1453.
- Shipley, G.P., Kindscher, K., 2016. Evidence for the paleoethnobotany of the Neanderthal: a review of the literature. *Scientifica* 8927654. <https://doi.org/10.1155/2016/8927654>.
- Shipman, P., 1984. Early hominid lifestyle: the Scavenging Hypothesis. *Anthroquest* 28, 9–10.
- Shipman, P., 2010. *The Animal Connection and Human Evolution*. Current Anthropology 51 (4), 519–538.
- Shipman, P., 2015a. *The Invaders*. Harvard University Press, Cambridge (MA), *How Humans and Their Dogs Drove Neanderthals to Extinction*.
- Shipman, P., 2015b. How we hunted out the Neanderthals. *New Sci.* 225, 26–27.
- Shryock, A., Trautmann, T.A., Gamble, C., 2011. *Imagining the Human in Deep Time*. In: Shryock, A., Smail, D.L. (Eds.), *Deep History*. University of California Press, Berkeley, *The Architecture of Past and Present*, pp. 21–52.
- Sick, H., 1997. *Ornitologia Brasileira*. Editora Nova Fronteira, Rio de Janeiro.
- Silk, J.B., 2019. Hyena politics: the dynamics of dynasties. *Proc. Natl. Acad. Sci. USA* 116 (18), 8644–8645.
- Simonova, V.V., 2018. The wild at home and the magic of contact. Stories about wild animals and spirits from Amudisy Evenki hunters and reindeer herders. *Études mongoles et sibériennes, centrasiatiques et tibétaines* 49, DOI: 10.4000/emscat.3505. (<http://journals.openedition.org/emscat/3505>).
- Skeates, R., 2017. Towards an archaeology of everyday aesthetics. *Cambridge Archaeol. J.* 27 (4), 607–616.
- Skinner, P.J., 2012. Relational cohesion in palaeolithic Europe: hominin-cave Bear interactions in Moravia and Silesia, Czech Republic, during OIS3. *British Archaeological Reports International Series* 2379, Oxford.
- Slimak, L., 2019. For a cultural anthropology of the last Neanderthals. *Quat. Sci. Rev.* 217 (1), 330–339.
- Smith, G.M., 2015. Neanderthal megafaunal exploitation in Western Europe and its dietary implications: a contextual reassessment of La Cotte de St Brelade (Jersey). *J. Hum. Evol.* 78, 181–201.
- Soffer, O., 1985. Storage, sedentism and the Eurasian Palaeolithic record. *Antiquity* 63, 719–732.
- Soffer, O., Adovasio, J.M., Kornietz, N.L., Velichko, A.A., Gribchenko, Y.N., Lenz, B.R., Sunsto, V.Y., 1996. Cultural stratigraphy at Mezhirich, an Upper Palaeolithic site in Ukraine with multiple occupations. *Antiquity* 71, 48–62.
- Sommerville, K., 2021. *Humans and Hyenas. Monster or Misunderstood*, Routledge, London.
- Snow, L., 2020. Poisoned, potent, painted: arrows as indexes of personhood. In: Wingfield, C., Giblin, J., King, R. (Eds.), *The pasts and presence of art in South Africa: Technologies, ontologies and agents*. McDonald Institute for Archaeological Research, Cambridge, pp. 31–39.
- Soressi, M., Hays, M.A., 2003. Manufacture, transport and use of Mousterian bifaces. A case study from the Perigord (France). In: Soressi, M., Dibble, H.L. (Eds.), *Multiple approaches to the study of bifacial technologies*. University of Pennsylvania Museum Press, Philadelphia, pp. 125–147.
- Soressi, M., Rendu, W., Texier, J.-P., Claud, E., Daulny, L., d'Errico, F., Laroulandie, V., Maureille, B., Niclot, M., Schwartz, S., Tillier, A.M., 2008. Pech-de-l'Azé I (Dordogne, France): Nouveau regard sur un gisement moustérien de tradition acheuléenne connu depuis le XIXe siècle. In: *Les sociétés Paléolithiques dans un grand Sud-Ouest: Nouveaux gisements, nouveaux résultats, nouvelles méthodes*, Société Préhistorique Française, Talence, France, 24–25 Novembre 2006. Société préhistorique française, Paris, pp. 95–132.
- Soriano, S., 2000. *Outils bifaciaux et outillage sur éclat au Paléolithique ancien et moyen: coexistence et interaction*. Doctoral Dissertation, University of Paris X – Nanterre.
- Soulier, M.-C., Costamagno, S., 2018. Le stockage alimentaire chez les chasseurs-cueilleurs paléolithiques. *Techniq. Cult.* 69, 88–103. <https://doi.org/10.4000/tc.8810>.
- Spagnolo, V., Crezzini, J., Marciani, G., Capecci, G., Arrighi, S., Aureli, D., Ekberg, I., Scaramucci, S., Tassoni, L., Boschin, F., Moroni, A., 2020. Neanderthal camps and hyena dens. Living floor 150A at Grotta dei Santi (Monte Argentario, Tuscany, Italy). *Journal of Archaeological Science: Reports* 30, 102249.
- Speth, J.D., 2004. News flash: negative evidence convicts Neanderthals of gross mental incompetence. *World Archaeol.* 36 (4), 519–526.
- Speth, J.D., 2017. Putrid Meat and Fish in the Eurasian Middle and Upper Paleolithic: Are We Missing a Key Part of Neanderthal and Modern Human Diet? *PaleoAnthropology* 2017, 44–72.
- Speth, J.D., Clark, J.L., 2006. Hunting and overhunting in the Levantine Late Middle Palaeolithic. *Before Farming* 3, 1–42.
- Spikins, P., Needham, A., Tilley, L., Hitchens, G., 2018. Calculated or caring? Neanderthal healthcare in social context. *World Archaeol.* 50 (3), 384–403.

- Stanton, D.W.G., Alberti, F., Plotnikov, V., Androsov, S., Grigoriev, S., Fedorov, S., Kosintsev, P., Nagel, D., Vartanyan, S., Barnes, I., Barnett, R., Ersmark, E., Döppes, D., Gernonpré, M., Hofreiter, M., Rosendahl, W., Skoglund, P., Dalén, L., 2020. Early Pleistocene origin and extensive intra-species diversity of the extinct cave lion. *Sci. Rep.* 10, 12621. <https://doi.org/10.1038/s41598-020-69474-1>.
- Steeves, P.F.C., 2021. The Indigenous Paleolithic of the Western Hemisphere. University of Nebraska Press, Lincoln.
- Stewart, J.R., 2005. The ecology and adaptation of Neanderthals during the non-analogous environment of Oxygen Isotope Stage 3. *Quat. Int.* 137, 35–46.
- Stewart, J.R., 2007. Neanderthal extinction as part of the faunal change in Europe during Oxygen Isotope Stage 3. *Acta zoologica cracoviensia* 50A (1–2), 93–124.
- Stewart, K., 2010. Worlding Refrains. In: Gregg, M., Seigworth, G. (Eds.), *The Affect Theory Reader*. Duke University Press, London, pp. 339–353.
- Stiner, M.C., 1991. The Faunal Remains From Grotta Guattari: A Taphonomic Perspective. *Current Anthropology* 32 (2), 103–117.
- Stiner, M.C., 1994. Honor Among Thieves: A Zooarchaeological Study of Neanderthal Ecology. Princeton University Press, Princeton (NJ).
- Stiner, M.C., 1999. Cave Bear Ecology and Interactions with Pleistocene Humans. *Ursus* 11, 41–58.
- Stiner, M.C., 2002. Carnivory, Coevolution, and the geographic spread of the genus *Homo*. *J. Archaeol. Res.* 10 (1), 1–63.
- Stiner, M.C., 2004. Comparative ecology and taphonomy of spotted hyenas, humans, and wolves in Pleistocene Italy. *Rev. Paléobiol.* 23 (2), 771–785.
- Stiner, M.C., 2012. Competition theory and the case for Pleistocene hominin-carnivore co-evolution. *J. Taphon.* 10 (3), 129–145.
- Stiner, M.C., Kuhn, S.L., 2006. Changes in the 'connectedness' and resilience of Paleolithic societies in Mediterranean ecosystems. *Human Ecol.* 34 (5), 693–712.
- Stringer, C.B., Finlayson, J.C., Barton, R.N.E., Fernández-Jalvo, Y., Cáceres, I., Sabin, R.C., Rhodes, E.J., Currant, A.P., Rodríguez-Vidal, J., Giles-Pacheco, F., Riquelme-Cantal, J.A., 2008. Neanderthal exploitation of marine mammals in Gibraltar. *Proc. Natl. Acad. Sci. USA* 105 (38), 14319–14324.
- Straus, L.G., 1982. Carnivores and cave sites in Cantabrian Spain. *J. Anthropol. Res.* 38, 75–96.
- Stuart, A.J., Lister, A.M., 2007. Patterns of Late Quaternary megafaunal extinctions in Europe and northern Asia. *Courier – Forschungsinstitut Senckenberg* 259, 287–297.
- Sultan, S., 2015. Organism and Environment Ecological Development, Niche Construction, and Adaptation Oxford University Press, New York.
- Svoboda, J., 2003. The Bohunician and the Aurignacian. In: Zilhão, J., d'Errico, F. (Eds.), *The Chronology of the Aurignacian and of the Transitional Technocomplexes: Dating, Stratigraphies, Cultural Implications*. Trabalhos de Arqueologia 33, Lisboa, pp. 123–131.
- Swanson, H.A., Lien, M.E., Ween, G.B. (Eds.), 2018. *Domestication Gone Wild. Politics and Practices of Multispecies Relations*. Duke University Press, Duke/London.
- Sykes, N., Beirne, P., Horowitz, A., Jones, I., Kalof, L., Karlsson, E., King, T., Litwak, H., McDonald, R.A., Murphy, L.J., Pemberton, N., Promislow, D., Rowan, A., Stahl, P.W., Tehrani, J., Tourigny, E., Wynne, C.D.L., Strauss, E., Larson, G., 2020. Humanity's best friend: a dog-centric approach to addressing global challenges. *Animals* 10 (3), 502–530.
- Tafelmaier, Y., 2011. Revisiting the Middle Palaeolithic site Volkringhauser Höhle (North Rhine-Westphalia, Germany). *Quartar* 58, 153–182.
- TallBear, K., 2011. Why interspecies thinking needs indigenous standpoints. *Cult. Anthropol.* 24. <https://culanth.org/fieldsights/why-interspecies-thinking-needs-indigenous-standpoints>.
- Tapner, R.L., 1988. Animality, Humanity, Morality and Society. In: Ingold, T. (Ed.), *What is an Animal?* Unwin Hyman, London, pp. 47–62.
- Tavoso, A., 1987. Le Moustérien de la grotte Tournal. *Cypselia* VI 161–174.
- Tchernov, E., 1984. Commensal Animals and Human Sedentism in the Middle East. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals in Archaeology 3. Early Herders and their Flocks* BAR Publishing, Oxford, pp. 91–115.
- Testart, A., 2012. *Avant l'histoire. L'évolution des sociétés, de Lascaux à Carnac*. Gallimard, Paris.
- Thieme, H., Veil, S., 1985. Neue Untersuchungen zum eemzeitlichen Elefanten-Jagdplatz Lehringen. *Ldkr. Verden. Die Kunde* 36, 11–58.
- Tilley, L., 2015. *Theory and Practice in the Bioarchaeology of Care*. Bioarchaeology and Social Theory, Springer, Cham.
- Todd, Z., 2014. Fish pluralities: Human-animal relations and sites of engagement in Paulatuuq, Arctic Canada. *Etudes/Inuit/Studies* 38 (1–2), 217–238.
- Todd, Z., 2017. Fish, Kin, and Hope: Tending to water violations in amiskwaciwáskahikan and Treaty Six Territory. *Afterall: A J. Art Context Inquiry* 43 (1), 102–107.
- Torres, T., Ortiz, J.E., Cobo, R., De Hoz, P., García-Redondo, A., Grün, R., 2007. Hominid exploitation of the environment and cave bear populations. The case of Ursus spelaeus Rosenmüller-Heinroth in Amutxate cave (Aralar, Navarra-Spain). *J. Hum. Evol.* 52, 1–15.
- Tournepiche, J.-F., 1994. Un néandertalien dévoré par des hyènes: La grotte de Rochelot (Saint-Amand de Bonniere, Charente). *Paléo* 6, 319–321.
- Treves, A., Palmquist, P., 2007. Reconstructing hominin interactions with mammalian carnivores (6.0–1.8 ma). In: Gurskey-Doyen, S.L., Nekaris, A.K.I. (Eds.), *Primate anti-predator strategies*. Springer, New York, pp. 355–381.
- Trinkaus, E., Maki, J., Zilhão, J., 2007. Middle Paleolithic human remains from the Gruta da Oliveira (Torres Novas), Portugal. *Am. J. Phys. Anthropol.* 134, 263–273.
- Tsing, A., 2012. Unruly Edges: Mushrooms as Companion Species. *Environmental Humanities* 1 (1), 141–154.
- Turner, A., 1985. Extinction, speciation and dispersal in African larger carnivores, from the Miocene to recent. *S. Afr. J. Sci.* 81, 256–257.
- Turner, A., 1990. The evolution of the guild of larger terrestrial carnivores in the Plio-Pleistocene of Africa. *Geobios* 23, 349–368.
- Turner, A., 1995. The Villafranchian large carnivore guild: geographic distribution and structural evolution. *II Quaternario* 8, 349–356.
- Turner, A., 2009. The evolution of the guild of large Carnivora of the British Isles during the Middle and Late Pleistocene. *J. Quat. Sci.* 24 (8), 991–1005.
- Turner, A., Antón, M., Werdelin, L., 2008. Taxonomy and evolutionary patterns in the fossil Hyaenidae of Europe. *Geobios* 41, 677–687.
- Turner II, C.G., Ovodov, N.D., Pavlova, O.V., 2013. *Animal Teeth and Human Tools. A Taphonomic Odyssey in Ice Age Siberia*. Cambridge University Press, Cambridge.
- Turq, A., Roebroeks, W., Bourguignon, L., Faivre, J.P., 2013. The fragmented character of Middle Palaeolithic stone tool technology. *J. Hum. Evol.* 65 (5), 641–655.
- Tzedakis, P.C., Emerson, B.C., Hewitt, G.M., 2013. Cryptic or mystic? Glacial tree refugia in northern Europe. *Trends Ecol. Evol.* 28 (12), 696–704.
- Uthmeier, T., 2004. Micoquien, Aurignacien und Gravettien in Bayern Eine regionale Studie zum Übergang vom Mittel- zum Jungpaläolithikum Archäologische Berichte, Bonn.
- Uthmeier, T., 2006. Triumph über die Natur? Zum Bild vom Neandertaler als Elefantenjäger. *Archäologische Informationen* 29 (1&2), 17–34.
- Uthmeier, T., Hetzel, E., Heißig, K., 2018. Neandertaler im spätesten Mittelpaläolithikum Bayerns? Die JerzmanoviceSpitzen aus der Kirchberghöhle bei Schmägingen im Nördlinger Ries. *Bericht der Bayrischen Bodendenkmalpflege* 59, 19–27.
- Utrilla, P., Montes, L., 1986. Las Cuevas de los Moros de Gabasa (Huesca). I: el yacimiento Musteriense (Campañas de 1984 y 1985). *Bolskan*, 3–16.
- Utrilla, P., Montes, L., Blasco, F., Torres, T., Ortiz, J.E., 2010. La cueva de Gabasa revisada 15 años después: un cubil para las hienas y un cazadero para los Neandertales. *Zona Arqueológica* 13, 376–389.
- Utrilla, P., Mazo, C., Domingo, R., 2015. Fifty thousand years of prehistory at the cave of Abautz (Arraitz, Navarre): a nexus point between the Ebro Valley, Aquitaine and the Cantabrian Corridor. *Quat. Int.* 364, 294–305.
- Yirga, G., De longh, H.H., Leirs, H., Gebrihiwot, K., Deckers, J., Bauer, H., 2012. Adaptability of large carnivores to changing anthropogenic food sources: Diet change of spotted hyena (*Crocuta crocuta*) during Christian fasting period in northern Ethiopia. *J. Anim. Ecol.* 81, 1052–1055.
- Yravedra, J., Cobo, L., 2015. Neanderthal exploitation of ibex and chamois in Southwestern Europe. *J. Hum. Evol.* 78, 12–32.
- Val, A., Porraz, G., Texier, P.-J., Fisher, J.W., Parkinson, J., 2020. Human exploitation of nocturnal felines at Diepkloof Rock Shelter provides further evidence for symbolic behaviours during the Middle Stone Age. *Sci. Rep.* 10, 6424. <https://doi.org/10.1038/s41598-020-63250-x>.
- Valensi, P., Psathi, E., 2004. Faunal Exploitation during the Middle Palaeolithic in southeastern France and northwestern Italy. *Int. J. Osteoarchaeol.* 14 (3–4), 256–272.
- Valoch, K., 2013a. The current state of knowledge of the earliest period of the Palaeolithic. In: Vencl, S., Fridrich, J., Valoch, K. (Eds.), *The Prehistory of Bohemia 1: The Palaeolithic and Mesolithic*. Archeologický ústav AV ČR, Prague, pp. 51–58.
- Valoch, K., 2013b. The Early Palaeolithic Site of Stránká Skála I near Brno (Czechoslovakia). *Anthropologie* 51 (1), 67–86.
- Van Valkenburgh, B., Hayward, M.W., Ripple, W.J., Meloro, C., Roth, L.V., 2016. The impact of large terrestrial carnivores on Pleistocene ecosystems. *PNAS* 113 (4), 862–867.
- Varela, S., Lobo, J.M., Rodríguez, J., Batra, P., 2010. Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time. *Quat. Sci. Rev.* 29, 2027–2035.
- Villa, P., Soressi, M., 2000. Stone tools in carnivore sites: the case of Bois Roche. *J. Anthropol. Res.* 56 (2), 187–215.
- Villa, P., Roebroeks, W., 2014. Neanderthal Demise: An Archaeological Analysis of the Modern Human Superiority Complex. *PLoS ONE* 9 (4), e96424.
- Villa, P., Castel, J.-C., Beauval, C., Bourdillat, V., Goldberg, P., 2004. Human and carnivore sites in the European Middle Palaeolithic: Similarities and differences in the bone modification and fragmentation. *Revue de Paléobiologie de Genève* 23, 705–730.
- Villa, P., Sanchez-Goñi, M.F., Bescós, G.C., Grün, R., Ajas, A., Pimienta, J.C.G., Lees, W., 2010. The archaeology and paleoenvironment of an Upper Pleistocene hyena den: an integrated approach. *J. Archaeol. Sci.* 37, 919–935.
- Villa, P., Soriano, S., Pollarolo, L., Smriglio, C., Gaeta, M., D'Orazio, M., Conforti, J., Tozzi, C., 2020. Neandertals on the beach: Use of marine resources at Grotta dei Moscerini (Latium, Italy). *PLoS ONE* 15 (1), e0226690. <https://doi.org/10.1371/journal.pone.0226690>.
- Villaluenga, A., Castaños, P., Arrizabalaga, A., Mujika, J., 2012. Cave Bear (*Ursus spelaeus* Rosenmüller-Heinroth, 1794) and humans during the early Upper Pleistocene (Lower and Middle Palaeolithic) in Lezetxiki, Lezetxiki II and Astigarragako Koba (Basque country, Spain). Preliminary approach. *J. Taphonomy* 10, 521–543.
- Villaverde, V., Martínez-Valle, R., Guillem, P., Fumanal, M.P., 1996. Mobility and the role of small game in the Middle Paleolithic of the central region of the Spanish Mediterranean: a comparison of Cova Negra with other Paleolithic deposits. In: Carbonell, E., Vaquero, M. (Eds.), *The Last Neandertals, the First Anatomically Modern Humans: A Tale about the Human Diversity*. Universitat Rovira i Virgili, Tarragona, pp. 267–288.
- Viranta, S., Grandal d'Anglade, A., 2012. Late Pleistocene Large Mammal Paleocommunities: A Comparative Study Between Localities with Brown Bear (*Ursus arctos*), Cave bear (*U spelaeus*) and Mousterian Lithic Assemblage. *J. Taphonomy* 10 (3–4), 265–276.

- Viveiros de Castro, E., 1996. Images of nature and society in amazonian ethnology. *Ann. Rev. Anthropol.* 25, 179–200.
- Von Königswald, W., Müller-Beck, H., 1975. Das Pleistozän der Weinberghöhlen bei Mauern (Bayern). *Fossil-Vergesellschaftungen* Nr. 35. *Quartär* 26, 107–118.
- Walker, M.J., López-Martínez, M.V., Ortega-Rodríguez, J., Haber-Uriarte, M., López-Jiménez, A., Avilés-Fernández, A., Polo-Camacho, J.L., Campillo-Boj, M., García-Torres, J., Carrión García, J.S., San Nicolás-del Toro, M., Rodríguez-Estrella, T., 2012. The excavation of buried articulated Neanderthal skeletons at Sima de las Palomas (Murcia, SE Spain). *Quaternary International* 259, 7–21.
- Wallach, A.D., Ripple, W.J., Carroll, S.P., 2015. Novel trophic cascades: apex predators enable coexistence. *Trends Ecol. Evol.* 30 (3), 146–153.
- Walls, M., 2019. The bow and arrow and early human sociality: an enactive perspective on communities and technical practice in the middle stone age. *Philos. Technol.* 32 (2), 265–281.
- Walsh, D.M., 2015. *Organisms, Agency, and Evolution*. Cambridge University Press, Cambridge.
- Watanabe, S., 2012. Animal Aesthetics from the Perspective of Comparative Cognition. In: Watanabe, S., Kuczaj, S. (Eds.), *Emotions of Animals and Humans: Comparative Perspectives*. Springer, Tokyo, pp. 129–162.
- Watts, C., 2013a. *Relational Archaeologies: Humans, Animals, Things*. Routledge, London.
- Watts, V., 2013b. Indigenous place-thought & agency amongst humans and non-humans (First Woman and Sky Woman go on a European world tour!). *Decolonization: Indigeneity, Education & Society* 2 (1), 20–34.
- Weedman Arthur, K., 2018. *The Lives of Stone Tools. Crafting the Status, Skill, and Identity of Flintknappers*. The University of Arizona Press, Tucson.
- Weiss, M., 2020. The Lichtenberg Keilmesser - it's all about the angle. *PLoS ONE* 15, e0239718. <https://doi.org/10.1371/journal.pone.0239718>.
- Welsch, W., 2004. Animal aesthetics. *Contemporary Aesthetics* 2 (1), 15.
- Werdelin, L., Lewis, M.E., 2005. Plio-Pleistocene Carnivora of eastern Africa: Species richness and turnover patterns. *Zool. J. Linnean Soc.* 144, 121–144.
- White, M.J., Pettitt, P., 2011. The british late middle palaeolithic: an interpretative synthesis of neanderthal occupation at the northwestern edge of the pleistocene world. *J. f World Prehistory* 24, 25–97.
- White, M.J., Pettitt, P., Schreve, D., 2016. Shoot first, ask questions later: Interpretative narratives of Neanderthal hunting. *Quat. Sci. Rev.* 140, 1–20.
- Widlok, T., 2018. Lions and Flies: Forager-Animal Situations. In: Breyer, T., Widlok, T. (Eds.), *The Situationality of Human-Animal Relations. Perspectives from Anthropology and Philosophy*, Transcript, Bielefeld, pp. 203–220.
- Widlok, T., 2020. Sharing, presence and the built environment. *Built Environ.* 46 (1), 28–39.
- Wilkins, J., Schoville, B.J., Pickering, R., Gliganic, L., Collins, B., von der Brown, K.S., Meden, J., Khumalo, W., Meyer, M.C., Maape, S., Blackwood, A.F., Hatton, A., 2021. Innovative *Homo sapiens* behaviours 105,000 years ago in a wetter Kalahari. *Nature* 592, 248–252.
- Willerslev, R., 2007. *Soul Hunters: Hunting, Animism, and Personhood Among the Siberian Yukaghirs*. University of California Press, Berkeley.
- Willerslev, R., Ulturgasheva, O., 2012. Revisiting the Animism Versus Totemism Debate: Fabricating Persons Among the Eveny and Chukchi of North-Eastern Siberia. In: Brightman, M., Grotti, V.E., Ulturgasheva, O. (Eds.), *Animism in Rainforest and Tundra: Personhood, Animals, Plants and Things in Contemporary Amazonia and Siberia*. Berghahn Books, New York, pp. 48–68.
- Wisher, I., Kay, K., 2020. *Animal-Human Interactions: Becoming, Creating, Relating*. In: Kaercher, K., Arntz, M., Bomentre, N., Hermoso-Buxán, X.L., Kay, K., Ki, S., Macleod, R., Muñoz-Mojado, H., Timbrell, L., Wisner, I. (Eds.), *New Frontiers in Archaeology*. Archaeopress, Oxford, pp. 129–135.
- Wojtal, P., Svoboda, J., Roblíčková, M., Wilczyński, J., 2020. Carnivores in the everyday life of Gravettian hunters-gatherers in Central Europe. *J. Anthropol. Archaeol.* 59, 101171.
- Wolch, J., Emel, J., 1998. *Animal Geographies: Place, Politics, and Identity in the Nature-Culture Borderlands*. Verso, London/New York.
- Wolfe, C., 2011. Moving forward, kicking back: The animal turn. *Postmedieval: a journal of medieval cultural studies* 2, 1–12.
- Wood, R.E., Barroso-Ruiz, C., Caparrós, M., Jordá Pardo, J.F., Galván Santos, B., Higham, T.F.G., 2013. Radiocarbon dating casts doubt on the late chronology of the Middle to Upper Palaeolithic transition in southern Iberia. *Proc. Natl. Acad. Sci.* 110, 2781–2786.
- Woodburn, J., 1980. Hunters and gatherers today and reconstruction of the past. In: Gellner, E. (Ed.), *Soviet and Western anthropology*. Duckworth, London, pp. 95–117.
- Woodburn, J., 1982. *Egalitarian Societies*. *Man* 17 (3), 431–451.
- Wragg Sykes, R., 2017. Neanderthals in the outermost West: technological adaptation in the Late Middle Palaeolithic (re-)colonization of Britain, Marine Isotope Stage 4/3. *Quat. Int.* 433, 4–32.
- Wragg Sykes, R., 2020. *Kindred. Neanderthal Life, Love, Death, and Art*. Bloomsbury, London.
- Zahara, R.D., Hird, M.J., 2015. Raven, dog, human: inhuman colonialism and unsettling cosmologies. *Environ. Humanities* 7, 169–190.
- Zehnle, 2015. Of Leopards and Lesser Animals. Trials and Tribulations of the 'Human-Leopard Murders' in Colonial Africa. In: Nance, S. (Ed.), *The Historical Animal*. Syracuse University Press, New York, pp. 221–238.
- Zilhão, J., 2009. Szeletian, Not Aurignacian: A Review of the Chronology and Cultural Associations of the Vindija G1 Neandertals. In: Camps, M., Chauhan, P. (Eds.), *Sourcebook of Paleolithic Transitions. Methods, Theories, and Interpretations*. Springer, New York, pp. 407–426.
- Zilhão, J., Angelucci, D., Argant, J., Brugal, J.-P., Carrión, J.S., Carvalho, R., Fuentes, N., Nabais, M., 2010. Humans and hyenas in the middle Paleolithic of Gruta da Oliveira (Almonda karstic system, Torres Novas, Portugal). In: *1a Reunión de científicos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península*, pp. 299–308.
- Zilhão, J., Angelucci, D.E., Arnold, L.J., d'Errico, F., Dayet, L., Demuro, M., Deschamps, M., Fewlass, H., Gomes, L., Linscott, B., Matias, H., Pike, A.W.G., Steier, P., Talamo, S., Wild, E.M., 2021. Revisiting the Middle and Upper Palaeolithic archaeology of Gruta do Caldeirão (Tomar, Portugal). *PLoS ONE* 16 (10), e0259089.
- Zilio, L., Hammond, H., Karampaglidis, T., Sánchez-Romero, L., Blasco, R., Rivals, F., Rufá, A., Picin, A., Chacón, M.G., Demuro, M., Arnold, L.J., 2021. Examining Neanderthal and carnivore occupations of Teixoneres Cave (Moià, Barcelona, Spain) using archaeostratigraphic and intra-site spatial analysis. *Sci. Rep.* 11 (1), 4339.