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WHAT WERE THEY UP AGAINST? LOWER PALEOLITHIC HOMININ MEAT ACQUISITION AND COMPETITION WITH PLIO-PLEISTOCENE CARNIVORES

Abstract

The habitual inclusion of meat into the diet was one of the most significant developments in hominin evolution. In addition to the nutritional benefits, competition with carnivores for animal resources was most likely a significant selective force in the Lower Paleolithic. In this paper, we provide a literature review of the origins of hominin meat acquisition. We address major debates that have shaped archaeologists' understanding of this topic (i.e., hunting versus scavenging, primary versus secondary acquisition) and synthesize the current state of the discussion. In addition to taphonomic data from zooarchaeological assemblages, we discuss evolutionary processes that were occurring in the carnivore guild during the Plio-Pleistocene, when we see the earliest evidence for meat acquisition by hominins. From the data currently available, we draw two main conclusions regarding meat procurement by hominins. The first is that, though scientists have documented earlier cases, there seems to be a marked increase in evidence for meat acquisition between 1.8 and 1.5 Ma in both Africa and Eurasia. It is possible that early hominins used a combination of passive and confrontational scavenging to access meat during this period, and we do not exclude the possibility that they also occasionally hunted. The second conclusion is that after 500,000 BP, we see extremely strong evidence for hominin hunting. This also might have occurred before this time, but there are more examples after this time period over a wide geographic range. We do not see these shifts as a strict linear progression, but rather as a mosaic of different strategies that began at different times in multiple locations. Based on the meat acquisition strategies of many carnivore species, in addition to modern hunter-gatherers, we, like many authors, do not see hunting and scavenging as an all-or-nothing-prospect, but rather as a continuum that shifts depending on the circumstances. We also discuss some differences in interpretations made by zooarchaeologists that seem to be more closely related to the time period (pre- or post-1.0 Ma) or geographical region (Eurasia or Africa) in which scientists are working, as opposed to the actual archaeological record.

Keywords

Lower Paleolithic / Early Stone Age, zooarchaeology, taphonomy, mortality profiles, carnivore guild

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Introduction

The inspiration for this paper came from the session "A diachronic perspective of human behavioural adaptations to interglacial lakeshore environments during the European Pleistocene to early Holocene" at the 2014 UISPP conference held in Burgos, Spain. The session focused on the importance of lakeshore environments as critical ecosystems for hominins and as favorable preservation settings of archaeological sites. As we listened to the different presentations, particularly those on the Lower Paleolithic sites of Miesenheim I and Schöningen, we thought about the many other important Eurasian interglacial lakeshore sites from this period (e. g. Gesher Benot Ya'aqov, Israel; Hoxne, England; Torralba, Spain). Part of our ongoing work at Schöningen highlights the importance of lakeshore environments, not only for hominins, but also for carnivores that exploit such ecosystems for water and prey (e. g. Serangeli et al. 2015; Starkovich/Conard 2015), meaning that lakeshores are prime areas for competition between hominins and carnivores. We are certainly not the first to make this connection; a particularly large body of Lower Paleolithic research addressing this topic (at least implicitly) comes from the east African sites of Olduvai Gorge (Tanzania) and Koobi Fora (Kenya) (see below). So we began to review the literature in order to understand the current ideas surrounding hominin meat acquisition, and the role that hominin-carnivore interactions played in the origins of meat-eating for the genus *Homo*. We quickly realized 1) that it had been some time since archaeologists had presented a review on this topic for Africa or Eurasia (e. g. Gifford-Gonzalez 1999; Domínguez-Rodrigo 2002; Stiner 2002; Domínguez-Rodrigo/Pickering 2003), and 2) it would be remiss of us to exclude iconic cave and rock shelter sites such as those in the Sierra de Atapuerca (Spain) or Dmanisi (Georgia), simply because they are not on a lakeshore, or Boxgrove (England) and Ambrona (Spain) because they preserved glacial deposits.

Therefore, we decided to expand our initial focus on carnivore-hominin competition at lakeshore localities to explore the larger picture of hominins entering the carnivore guild during the Plio-Pleistocene, though lakeshore sites still hold a prominent place in this discussion. We provide an in-depth review of Lower Paleolithic sites in Africa and Eurasia that yield evidence of meat eating to evaluate the extent to which hominins had access to animal tissues and to test whether or not there are any clear chronological shifts that might signal the origins of hunting. We consider these behaviors in the context of other large-bodied carnivores on the landscape with which hominins had competitive and co-evolutionary relationships. We end the review around 300,000 BP. This date is semi-arbitrary; we chose it because it is the date of the Spear Horizon at Schöningen, one of the late interglacial lakeshore sites that sparked this paper, and a site that we are both intimately familiar with (see papers in Conard et al. 2015a). It is also a logical endpoint because Schöningen is among the oldest sites with unequivocal evidence for hominin hunting (Thieme 1997; Voormolen 2008; Conard et al. 2015b). Though the site has a strong anthropogenic signature, there is also ample evidence for large-bodied carnivores such as wolves (*Canis lupus*) and sabertooth cat (*Homotherium latidens*) modifying the bones. This is a strong reminder that even by the time hominins had clearly entered the predatory guild, they were still competing with carnivores, particularly when it came to issues such as settlement patterns and carcass butchery.

As we know well, modern humans have the ability to control and manipulate their environments to an extent that is unprecedented in the animal kingdom. This ranges from large-scale processes such as deforestation, coastline maintenance with levees and dykes, industrial agriculture, and the rerouting of major rivers through irrigation, to smaller, more local processes. A modern example of the latter is the ongoing conflict between humans and predators over livestock or game animals, which has resulted in myriad responses: predator suppression, the release of farm-raised game, translocation, or even diversionary feeding (see review in Graham/Beckerman/Thirgood 2005). This treatment of predators is actually a fairly recent phenomenon that has its roots in the domestication of ungulates, when the very livelihood of pastoral groups was suddenly threatened by large carnivores such as wolves, tigers, lions, and hyenas (e.g. Diamond 1989). And while the relationship between large carnivores and humans was not always so unbalanced in favor of human control, tension between the groups has existed for millennia. The connection between large-bodied carnivores and humans is unique because it transcended boundaries from a time when hominins fell victim to carnivores, to direct and indirect competition for meat resources as part of the predator guild, to the eventual domestication of dogs. The next phase of this transition, the point at which hominins started incorporating a significant amount of meat in their diets and entered the predator guild, is at the heart of this paper. When this occurred is not known, but has evolutionary importance for our development as a species. By the Upper Paleolithic, it is clear that modern humans were successful hunters of a range of prey types. Even by the Middle Paleolithic of Eurasia and Middle Stone Age of Africa, hominins were at the top of the food chain. Evidence for this comes from increasingly complex toolkits, and an abundance of sites featuring a range of large ungulate prey species hunted in the prime of their lives (e.g. Gaudzinski 1995; Speth/Tchernov 1998; Gaudzinski/Roebroeks 2000; Stiner 2005; 2009; Adler et al. 2006; Costamagno et al. 2006; Speth/Clark 2006; Shea/Sisk 2010; Starkovich 2014; Niven et al. 2012; Rendu et al. 2012; Starkovich 2012a). The implications of this are that hominins entered the predator guild as competent hunters sometime during the Lower Paleolithic.

In Africa, early members of the genus *Homo* and late australopithecines incorporated meat into their diets as early as 2.6 million years ago (Ma), or possibly even 3.39 Ma (de Heinzelin et al. 1999; McPherron et al. 2010; Thompson et al. 2015). There were many paths to meat acquisition, and whether or not it initially involved hunting, passive scavenging, confrontational scavenging, or a combination of these strategies, early hominins had to contend with a complex and well-established predator guild. Interactions with carnivores would have followed multiple pathways, starting with hominin ancestors attempting not to fall victim to predators and behavioral modifications to maximize avoidance (i.e., diurnal activities as opposed to those at dusk or dawn when carnivores are most active), which developed into day-to-day competition for individual carcasses and predation of the same prey populations. Eventually, the position of hominins in the predator guild crystalized to the extent that by the Middle Paleolithic, hominins were successful hunters of large game on multiple continents. The route to this adaptation is of special interest to archaeologists and paleoanthropologists alike, as it was eventually accompanied by increases in cranial capacity, more advanced tool technologies, the adoption of fire, the origins of language, and widespread colonization.

Origins of Hominin Meat Eating

There are many questions surrounding the earliest use of meat by hominins. At the most basic level, there is the issue of when meat-eating began, and who started it. Based on our current knowledge, the earliest widely-recognized stone tools are found at Gona (Ethiopia) and date to 2.6-2.5 Ma, and the earliest accepted evidence for cut marks on bones come from the 2.5 Ma site of Bouri (Ethiopia) (de Heinzelin et al. 1999). A few scholars have questioned this paradigm in recent years, with the 3.3 Ma industry found at Lomekwi 3 (Kenya) (Harmand et al. 2015), and seemingly cut bones at Dikika (Ethiopia) which date to 3.39 Ma (McPherron et al. 2010; Thompson et al. 2015), though more work is needed in this early period. It is possible, and even likely, that the earliest stone tools were used for cutting materials other than meat, for example plants; though based on the roughly contemporaneous appearance of stone tools and cut bones, early stone tools probably served multiple functions. The question of who used the earliest tools is not entirely clear; scholars have implicated species of both *Homo* and *Australo-*

pithecus as the first manufacturers of stone tools (Semaw et al. 1997; de Heinzelin et al. 1999; McPherron et al. 2010; Harmand et al. 2015; Thompson et al. 2015), though this debate is beyond the scope of our paper. Moving into more advanced questions involving meat procurement and early hominins, there is the issue of how significant meat was to the diet of past hominins. Based on the current body of data, this is largely unknowable and we will not pursue the question further here. Central to our interests, is how did early hominins acquire meat (i. e., hunting or scavenging), and how did they interact with Plio-Pleistocene predators in Africa, and later in Eurasia. We would like to stress, however, that while the hunting / scavenging debate is important to our understanding of the past, these strategies certainly existed along a continuum, with shifting proportions of hunting and scavenging depending on the circumstances. While the introduction of meat into the diet had evolutionary significance from a nutritional standpoint, in the sense that easier digestion and the consumption of long fatty acid chains facilitated brain growth (Hayden 1981; Speth 1989; Eaton / Eaton III / Cordain 2002), we would argue that the entrance into the carnivore guild and competition with large predators was equally significant in terms of the social, technological, and cultural adaptations it required (see also Stiner 2002). As such, hominin-carnivore interactions at Plio-Pleistocene sites and order of access to meat is a key area of research at early Lower Paleolithic sites. In this section, we outline the state of research on early hominin meat acquisition, and discuss the African and Eurasian carnivores that helped shape the evolution of our hominin ancestors.

Small game and aquatic resources

Though we will devote most of this discussion to the consumption of large game, it is increasingly apparent that early hominins exploited a range of prey types. A significant initial source of protein and fat might have come from aquatic resources, as researchers have documented in the Omo (Ethiopia) as early as 2.4 Ma, at Koobi Fora (Kenya) between 1.95 and 1.5 Ma, and at Olduvai Gorge (Tanzania) between 1.85 and 1.2 Ma (Chavaillon 1976; Stewart 1994; 2010; Pobiner 2007; Braun et al. 2010; Archer et al. 2014). All of these sites contain disproportionately high numbers of taxa such as turtles and especially catfish, some of which preserve evidence of cut marks (Stewart 1994; 2010; Pobiner 2007; Braun et al. 2010; Archer et al. 2014). The authors argue that at certain times of year, these taxa become sessile prey that are easily collected without any specialized hunting technologies. Specifically, catfish spawn in shallow pools during the dry season, and are vulnerable to becoming stranded. Because they have primitive lungs, they can live out of water for multiple days, providing an easily collected fresh aquatic food source for hominins and other animals (Stewart 2010; Archer et al. 2014). Access to this type of prey is important for two reasons. First, catfish are available in the late dry season, when ungulate fat stores are depleted. Second, aquatic resources provide docosahexaenoic acid and long-chain polyunsaturated fatty acids that are linked to brain growth in hominins (Broadhurst / Cunnane / Crawford 1998; Braun et al. 2010; Stewart 2010; Archer et al. 2014). Approaching this question from a theoretical standpoint, Joordens et al. (2009) introduced a model based on the ecological parameters of Trinil (Java) to predict that hominins should have exploited aquatic resources in that particular environment around 1.5 Ma. While they did not find direct evidence of hominin exploitation of marine resources at the site, though the shells are still under study, the authors point out that omnivorous mammals living in a coastal environment that have access to nutritious and catchable prey, such as shellfish or stranded catfish, inevitably exploit these resources (Joordens et al. 2009).

Evidence for the consumption of aquatic resources by early Lower Paleolithic hominins should come as no surprise to archaeologists; there is ample evidence of the exploitation of marine resources by modern primates including tarsiers, monkeys, macaques, baboons, orangutans, and bonobos (see reviews in Stewart et al. 2008; Kempf 2009; Stewart 2010; Russon et al. 2014). These authors, however, are quick to point out that the use of aquatic animals by modern primates is unusual, and fishing is even rarer. While there are a few documented cases of tool use for fishing (i. e., stick tools and food bait), most marine resources eaten by primates are easily gathered, including sessile catfish (Russon et al. 2014).

In terms of terrestrial small game, some of the earliest evidence of hominin exploitation of this prey type comes from cut hedgehog bones recovered from the 1.76 Ma layers at Olduvai Gorge Bed I (Tanzania) (Fernandez-Jalvo / Andrews / Denys 1999). Moving to the late Lower Paleolithic, Blasco et al. (2011) document the consumption of tortoises at Sima del Elefante (Atapuerca, Spain) between 1.2 and 0.78 Ma, along with cut marks on one bird and two leporid bones. Subsequent evidence of terrestrial small game use is rare until the Middle Paleolithic and Middle Stone Age, when tortoises became common in archaeological assemblages (e. g. Stiner / Munro / Surovell 2000; Speth / Tchernov 2002; Steele / Klein 2009; n. d.; Starkovich 2012b). An exception to this is at Gran Dolina (Atapuerca, Spain) and Bolmor Cave (Spain), where there is evidence for the exploitation of rabbits and birds in marine oxygen isotope stage (MIS) 9. The authors note multiple specimens with cut marks, and what they interpret as human gnaw marks (Blasco / Peris 2009; Blasco / Peris 2012; Blasco et al. 2013), though these kinds of observations are unusual at Middle Pleistocene sites.

As with other subsistence evidence from the Lower Paleolithic, it is unclear exactly what proportion of the diet aquatic resources and small terrestrial game comprised, though they undoubtedly contributed important nutrients to hominins with increasingly larger and more complex brains. Indeed, Stewart (2010) proposes that aquatic foods led to brain growth and tool use even before hominins exploited large, terrestrial mammals on a regular basis. The difficulties with testing this hypothesis, and with understanding the extent of small game use in general, is that sites yielding unambiguous evidence for small game exploitation from this time are still rare. New studies, as well as re-evaluations of old assemblages using new experimental data that specifically address the taphonomy of small animals (e. g. Archer / Braun 2013) are critical. For this reason, and because the major focus of this paper is the evolutionary pressure exerted by competition between carnivores and hominins (see Stewart 1994 for a discussion of expected low-levels of competition when it comes to aquatic resources), we now shift our focus to large-bodied game.

Megafauna

A particularly difficult to interpret aspect of the Lower Paleolithic faunal record is the use of megafauna, such as elephants, rhinoceros, and hippopotamus, by hominins. There are many instances of stone tools being found in association with proboscidean remains (e. g. Olduvai FLK North, Tanzania; Barogali, Djibouti; Southfleet Road, England; Notarchirico, Italy; Gesher Benot Ya-aqov, Israel; Kärlich-Seeufer, Germany) (Leakey 1971; Chavaillon et al. 1987; Goren-Inbar et al. 1994; Gaudzinski et al. 1996; Cassoli et al. 1999; Berthelet / Chavaillon 2001; Piperno / Tagliacozzo 2001; Wenban-Smith 2013), though few sites provide evidence for cut marks on bone (e. g. Olduvai SHK Main and BK, Tanzania; Buia, Eritrea; Revadim Quarry, Israel; Fuente Nueva-3, Torralba, Ambrona, and Áridos 2, Spain; La Polledrara di Cecanibbio and Castel di Guido, Italy) (Anzidei / Cerilli 2001; Fiore et al. 2004; Yravedra et al. 2010; Boschian / Saccà 2010; Domínguez-Rodrigo et al. 2010; 2014a; 2014b; Anzidei et al. 2012; Rabinovich et al. 2012; Saccà 2012; Espigares et al. 2013). Looking only at the latter set of sites, there is also the question of whether, or to what degree, Lower Paleolithic hominins hunted or scavenged megafauna.

This debate played out over nearly a decade between Lewis Binford on the one hand and Clark Howell and Leslie Freeman on the other. After excavating Torralba and Ambrona, Howell and Freeman suggested that early hominins were successful hunters of large game including megafauna (Howell 1963; 1966; Freeman Jr. / Butzer 1966; Freeman / Freeman 1975; Freeman Jr. 1978). Binford subsequently analyzed the data from Torralba and concluded that the remains mostly represented hominin scavenging from large carnivore kills (Binford 1987). In the meantime, Shipman and Rose (1983) used scanning electron microscopy to analyze the surfaces of the Torralba and Ambrona faunal remains, and only found a total of 16 cuts in both assemblages. Klein (1988) added to the debate with his own analysis, in which he argued that the mortality profiles of elephants at the two sites correspond more closely with attritional mortality, indicative of natural or accidental deaths, as opposed to a catastrophic profile expected by hominin hunting or game drives. The idea of examining mortality profiles turns out to be critical to our understanding of meat acquisition in the past and we will expand upon it further below. Based on additional excavations and data analysis at the sites, Howell and Freeman continued to argue that hominin hunters were responsible for the deaths of the elephants at Torralba and Ambrona. Further, they re-calculated Klein's mortality profiles and determined that the age representation was both catastrophic and attritional, lending further support to their original hunting scenario (Freeman 1994; Howell et al. 1995). In the most recent contribution to the debate, Villa et al. (2005) provide the results of a re-excavation at Ambrona. They find additional elephant remains with occasional traces of hominin activities in the form of cuts and spiral fractures. Carnivore gnawing is rare on the assemblage, and significantly, bone surface preservation is better than in the earlier studies (e. g. Shipman / Rose 1983). The authors conclude that due to the complexities of site stratigraphy and palimpsest nature of the deposits, Ambrona does not provide adequate evidence to support the scavenging hypothesis advocated by Binford, nor the hunting hypothesis supported by Howell and Freeman (Villa et al. 2005).

The back-and-forth nature of this debate is fairly typical for many important Lower Paleolithic sites, and is largely a product of the small number of well-preserved assemblages. This was particularly a problem in the 1980s and 90s, when the arguments were the most contentious. However, additional complicating issues are the fact that many sites occur near bodies of water (e. g. Gesher Benot Yaaqov, Torralba, Ambrona, FLK North, etc.). Such environments may contain a disproportionate number of mega-herbivores, as stressed elephants and rhinoceros seek out water in times of drought, or semi-aquatic hippopotamus die in their natural habitats. Another problem is the lack of direct evidence of hominin exploitation of carcasses from cuts or other butchery marks. Finally, many sites contain only one or a few animals, so it is difficult to establish meaningful mortality profiles for megafauna at Lower Paleolithic sites, and these profiles could indicate the likelihood that animals were hunted or scavenged. With the small amount of data currently available, some authors argue that mostly prime-aged adults are typically represented, which indicates hominin hunting (e. g. Wenban-Smith 2013), while others contend that the vulnerable old and young are typically found (e. g. Gaudzinski et al. 2005). At this stage, until a synthesis of a large number of stratigraphically intact, well-studied sites is available, the most meaningful conclusion that we can draw is that Lower Paleolithic hominins occasionally consumed the meat of megafauna. Whether this was through coordinated hunting efforts, the scavenging of carcasses that then had to be protected from carnivores, or some combination of both, is behaviorally important. However, the available data are insufficient to address this question conclusively. Data from smaller-bodied herbivores currently provide the greatest potential to address the origins of meat procurement and consumption.

Hunting among non-human primates

Before we turn our discussion to early evidence for hominin meat acquisition, it is useful to address the meat eating behaviors of non-human primates. Of course, modern primates are not an analog for past hominins, but they are important to provide a frame of reference for understanding the evolution of modern human hunting behaviors, which are far from the norm compared to our primate relatives. As we have touched on above, primates are known to consume animal protein in the form of marine or terrestrial resources. Scientists have also documented hunting behaviors among baboons, chimpanzees, and bonobos, which exploit taxa such as monkeys, young gazelles, bushpigs, bushbucks, forest antelope, hares, squirrels, and rodents (e. g. Harding 1973; 1974; Harding / Strum 1976; Hausfater 1976; Wrangham 1977; Morris / Goodall 1977; Hamilton / Bussne 1978; Strum 1981; Stanford et al. 1994; Stanford 1995; Watts / Mitani 2002; Surbeck / Hohmann 2008). However, hunting is uncommon among primates (and scavenging is even more unusual), and no taxa even approach the amount of meat eating we see among modern humans (C. Boesch / H. Boesch 1989; Stanford et al. 1994). Another relevant point concerning primate hunting is that primates rarely engage with prey that are larger or have similar body sizes to their own (McGrew 2001; Rose 2001; Stanford 2001). So while at least three other species of primate incorporate meat into their diets, it is at a very different scale than what we see with modern humans. It is unclear how the quantity of meat compares to that eaten by earlier hominins, but at least in terms of the body sizes of prey it is quite different, as we will now discuss.

Evidence pre-1.0 Ma

Most of the data we have regarding hominin subsistence strategies from the early part of the Lower Paleolithic come from a small number of Early Stone Age fossil accumulations from East Africa, namely Olduvai Gorge and Koobi Fora. Numerous scholars have analyzed, reanalyzed, and debated the meaning of these assemblages for nearly half a century. A central question in these studies is whether hominins or carnivores had primary access to large mammal remains at a small number of preserved sites that are more than a million years old. This is particularly the case at FLK Zinj (1.75 Ma, Olduvai Gorge), where zooarchaeologists and taphonomists have tried to understand the nature of the remains since the early 1980s. Before this, the dominant paradigm was that many Oldowan sites represented a “home base” on the landscape, where male hominins brought meat that was provisioned to females and other members of the group (Isaac 1971; 1978; 1984). Similar to the discussion surrounding Torralba and Ambrona, this view was criticized by Binford, who argued that early hominins at FLK Zinj were marginal scavengers who passively accessed bone marrow from carnivore kills, only after the carcasses were already stripped of meat (Binford 1981; 1985; 1988; Binford / Blumenschine 1986). Initially analysts attempted to use the anatomical representation of ungulates present at sites to determine if the faunas were accumulated by hominins, and therefore if they had primary or secondary access to carcasses. This is problematic, however; while the majority of early Lower Paleolithic faunal assemblages are dominated by head and limb elements (Bunn / Kroll 1986; Bunn 1997), archaeologists have documented both humans and carnivores transporting limb bones away from kill sites (Binford 1981; Bunn 1983; 1991; Bunn / Kroll 1986), which can be used to support either side of the argument. Another complication is the fact that most of the early assemblages are heavily biased by taphonomic factors, including mechanical processes, chemical weathering, carnivore damage, and hominin butchery. These processes destroy structurally weak portions of bone, and render interpretations of the original composition of the assemblages and subsequent movement of elements to or from the site difficult or nearly impossible (Binford / Bertram 1977; Lyman 1984; 1994; Grayson 1989; Kreutzer 1992; Lam / Chen / Pearson 1999).

In the meantime, taphonomists conducted a range of actualistic studies and developed new quantification techniques and models in order to examine hominin and carnivore modifications on bones. This work, combined with bone surface damage and skeletal part ratios from Plio-Pleistocene sites, led Robert Blumenschine and colleagues to postulate that early Lower Paleolithic hominins primarily scavenged bone marrow from carnivore kills (Binford / Blumenschine 1986; Blumenschine 1986; 1988; 1991; 1995; Blumenschine / Marean 1993). In doing so, they created a formation model for the FLK Zinj faunas. First, leopards killed or scavenged ungulates. After feeding, the cats abandoned the meatless bones, which were then collected by hominins who transported the remains to the site and broke them open for marrow. Once the hominins were done, hyenas gnawed the greasy cancellous bone ignored by hominins, extracting the last nutrients from the remains. Blumenschine and colleagues based these conclusions on a large number of bite marks on midshafts, ample hammerstone fractures, and extensive gnawing on longbone epiphyses, which were consistent with marks these authors recorded during feeding experiments with carnivores (Binford/Blumenschine 1986; Blumenschine 1986; 1988; 1991; 1995; Blumenschine/Marean 1993; Selvaggio 1994; Capaldo 1997; 1998a; 1998b; Selvaggio/Wilder 2001; Pante et al. 2012). Due to the often ambiguous nature of cut mark damage, these butchery indicators were typically excluded from the formation models.

From the beginning, Henry Bunn argued that hominins had early access to ungulate carcasses, based on his analysis of the FLK Zinj and FxJj 50 (1.6 Ma, Koobi Fora) assemblages (Bunn et al. 1980; Bunn 1983; 1991; 1997; 2007; Bunn/Kroll 1986; Bunn/Ezzo 1993). Over the years, several authors have challenged him on this point, most notably Binford and later Blumenschine and colleagues, both of whom we discussed previously. In his work on the FLK Zinj and FxJj 50 faunas, Bunn's arguments supporting early hominin access to carcasses hinges on the kinds of taxa found at the sites and their respective skeletal portions, as well as the number and location of cut marks on the bones (Bunn et al. 1980; Bunn/Bartram/Kroll 1988; Bunn 1983; 1991; 1997; 2001; 2007; Bunn/Kroll 1986; Bunn/Ezzo 1993). For the first point, he notes that there are cut marks on animals of all sizes at the sites, including elephants and hippos. The lack of axial elements in the assemblages leads him to interpret the localities as central places where hominins brought meat-bearing bones, probably to share with other members of the group. Bunn also notes the presence of gazelle-sized ungulates in the assemblages, and argues that large-bodied carnivores tend to completely consume animals in this size class, increasing the likelihood that hominins accumulated these taxa.

Regarding butchery, Bunn highlighted both the number and location of cut marks, particularly at FLK Zinj, which tend to cluster near the major muscle attachments of long bones. Taking this analysis a step further, he compared the taphonomic signatures of these archaeological assemblages with modern butchery practices of the Hadza, and found the location of cut marks to be similar (Bunn/Bartram/Kroll 1988; Bunn 2001). Noting that the Hadza scavenge approximately 20 % of their meat, he proposed that similar to modern foragers, Plio-Pleistocene hominins might have engaged in a kind of "power scavenging", which involves confronting carnivores such as jackals, cheetahs, leopards, and lions, and chasing them from their kills. Bunn (2007) interprets the FLK Zinj and FxJj 50 assemblages as forming when hominins accessed prey, either through power scavenging in the case of large carcasses or hunting smaller-bodied ungulates, during the day, then carnivores had uninterrupted access to the same carcasses at night.

Additional data from other early Lower Paleolithic sites and subsequent work by Manuel Domínguez-Rodrigo and Travis Pickering has supported Bunn's earlier claims. Domínguez-Rodrigo, in particular, conducted complementary actualistic studies to those done by Blumenschine and colleagues, and found that large felids such as lions tend to deflesh ungulate carcasses when they have primary access to the point that no meat remains on the midshafts of long bones for hominins to remove (Domínguez-Rodrigo 1999a). Therefore, the very presence of cut marks on long bone shafts, particularly of the upper limbs, indicate that meat was present, and hominins had access to carcasses before felids (Domínguez-Rodrigo 1997; 1999b; 2002; Domínguez-Rodrigo/Bunn/Yravedra 2014). Furthermore, his work shows that when provided early access to a complete carcass, human butchery concentrates cut marks on the midshafts of the upper limb bones where the bulk of the muscle tissue is found. Conversely, in situations where carcasses are already largely defleshed, human cut marks focus on lower limb bones and the ends of long bone shafts. These experimental data support Bunn's observations of the FLK Zinj faunas.

Other recent studies that apply the actualistic observations developed over the last few decades seem to agree with Bunn's original hypothesis, that hominins started gaining early access to meat between about 2.0 and 1.5 Ma, and it became increasingly important after this time. Excavators interpret this to be the case at El-Kherba (Ain Hanech, Algeria), which dates to 1.8 Ma (Sahnouni et al. 2013), the 1.5 Ma Okote Member (Koobi Fora, Kenya) (Pobiner et al. 2008), and the ST Site Complex at Peninj (West Lake Natron, Tanzania), which also dates to 1.5 Ma (Domínguez-Rodrigo et al. 2002). All three of these sites preserve cut marks at locations on bones that are unexpected if the carcasses were already defleshed by carnivores. Pickering and colleagues (Pickering et al. 2004; 2007; 2008) have observed a similar pattern at Members 1 through 3 at Swartkrans (South Africa). The precise dating of these layers is problematic, but they all formed between 1.8 and 1.0 Ma. Multiple researchers working on Upper Bed II (Olduvai Gorge, Tanzania) have made similar arguments based on the location of percussion marks, cuts, and bites on bones in the 1.70-1.34 Ma layers (Monahan 1996; Egeland / Domínguez-Rodrigo 2008; Domínguez-Rodrigo et al. 2009; 2014a; 2014b); JK2, Upper Bed III (1.15-0.8 Ma) at the site also contains evidence of early meat access by hominins, from either hunting or confrontational scavenging (Pante 2013).

In moving past studies of anatomical representations and taphonomic data, Bunn and colleagues (Bunn / Pickering 2010; Bunn / Gurtov 2014) use mortality profiles based on ungulate teeth in order to determine if hominins were hunting at FLK Zinj. The earlier of these two papers is in response to the long-standing hunting versus scavenging debate, and a recent discussion between Bunn and colleagues (Pickering / Bunn 2007; Bunn / Pickering 2010) and Bramble, Lieberman and colleagues (Bramble / Lieberman 2004; Lieberman et al. 2007) regarding the possibility that the ability to run prey to the point of hyperthermic shock was an important selective advantage for early *Homo*. Initially, Bramble and Lieberman (2004) proposed that endurance running would allow hominins to acquire meat through persistence hunting or competitive scavenging. This was met with stark criticism by Pickering and Bunn (2007), who contend that the mixed savanna-woodlands in which early *Homo* evolved are not ideal for endurance running or tracking, and point out that the majority of modern groups that utilize this strategy are found in hot, dry, environments. In our opinion, one important outcome of this study is the way in which the authors investigate the possibility of hominin hunting in the Plio-Pleistocene, and more significantly, the presentation of bovid mortality profiles using updated methodology and data not available in earlier papers.

Bunn and Pickering (2010) compare mortality data from the FLK Zinj assemblage to accumulations from several modern carnivore taxa, and natural background faunas from Bed I at Olduvai Gorge as well as three South African sites (Swartkrans, Komdraai A, and Gondolin). Bunn and Gurtov (2014) expand the sample to include more Plio-Pleistocene archaeological assemblages, ethnographic data from the Hadza, and natural catastrophic wildebeest drowning events. The authors use tripolar graphs to compare the faunas by plotting the proportion of juvenile, prime-aged, and old adults in the assemblages, following Stiner (1990) and Steele and Weaver (2002). Previous authors have found that prime-aged adult or mixed prime-aged / juvenile assemblages tend to characterize hominin hunting patterns in the Middle Paleolithic through Holocene, which are significantly different from assemblages formed by carnivores (Stiner 1990; 1994; 2002; 2005). In the initial study, Bunn and Pickering (2010) find that the remains overlap with what is expected for a living structure or prime-aged adult mortality profiles. Based on this, along with fetal or neonate individuals and sex data for waterbucks, the authors conclude that hominins practiced a mixed strategy of power scavenging from felid kills along with the successful hunting of older male and pregnant or recently pregnant female waterbucks. In the updated study, Bunn and Gurtov (2014) contend that early *Homo* was a successful ambush hunter of large bovids. They find a similar pattern for gazelle- and antelope-sized bovids at FLK Zinj, though there is a slightly stronger old adult bias (Bunn/Pickering 2010).

Archaeologists have found far fewer sites that preserve fauna and predate 1.0 Ma outside of Africa. Exceptions to this are Dmanisi (1.77 Ma, Republic of Georgia) (Lordkipanidze et al. 2007), 'Ubeidiya (1.4 Ma, Israel) (Gaudzinski 2004), Sima del Elefante (1.22 Ma, Atapuerca, Spain) (Rodríguez et al. 2011; Huguet et al. 2013), and Vallonnet Cave (1.07-0.99 Ma, Alpes-Maritimes, France) (Echassoux 2004). At all of these sites, cut marks on ungulate long bones lead the authors to conclude that hominins had early access to meat. Some take their interpretations further and suggest that the remains represent evidence of hominin hunting. Huguet et al. (2013) postulate that hominins occupying Sima del Elefante employed a mixed strategy of hunting or confrontational scavenging, along with occasional passive scavenging, based on cut and impact marks on bones; Echassoux (2004) draws a similar conclusion at Vallonnet Cave. Gaudzinski (2004) interprets the relatively narrow range of species (i.e., cervids and equids) with cuts found within the context of more diverse background faunas at 'Ubeidiya as evidence of specialized hunting by hominins. In general, the zooarchaeological evidence from Eurasia is similar, though less abundant and less heavily scrutinized, than that from contemporary African sites, but the conclusions are largely similar to those set forth by Bunn and his colleagues.

The contributions that attempt to understand hominin subsistence in the Lower Paleolithic before 1.0 Ma make it clear that sites from this time period are difficult to interpret and probably represent a range of circumstances. Some of the assemblages are primarily carnivore accumulations, while others imply multiple possible modes of access to meat for hominins. The variation found at these sites probably characterizes the nature of hominin meat acquisition strategies in the earlier part of the Lower Paleolithic in fairly realistic terms; instead of an all-or-nothing model pitting hominins versus carnivores for primary access to carcasses, there were likely a number of different methods of meat procurement for millennia when hominins first began to venture into the carnivore niche. And indeed, many more sites must be discovered and analyzed before we can fully grasp the situation surrounding the earliest hominin meat acquisition strategies. Similar to modern hunter-gatherers, Plio-Pleistocene foragers likely adopted a number of tactics for acquiring meat, including passive or confrontational scavenging, and occasional hunting of certain taxa (O'Connell/Hawkes/Jones 1988). Following decades of debate surrounding the location of bite marks, cut marks, and impacts, many of these studies illustrate the fact that interpretations are difficult to make without a full suite of taphonomic data. Further, we suggest that constructing mortality patterns of herbivores, such as those attempted by Bunn and colleagues (Bunn/Pickering 2010; Bunn/Gurtov 2014), are key to making the analytical leap from whether hominins were scavenging carcasses to fairly convincing evidence for hunting.

Evidence post-1.0 Ma

In the late Lower Paleolithic, after 1.0 Ma, there are far fewer well-studied African faunal assemblages, both compared to earlier times, and the same period in Eurasia. One such example is Elandsfontein (Western Cape Province, South Africa). This particular site preserves a hominin skullcap and Acheulean tools, yet it is poorly dated; Klein and colleagues (2007) place its formation between 1.0 Ma and 600,000 BP based on biostratigraphic comparisons. The authors note that the proportion of cut marks is fairly low (0.2 %) so the faunas were probably accumulated and modified by carnivores as opposed to hominins. Further, Klein et al. (2007) explore mortality profiles of zebras and cape buffalo, the two most common taxa at the site. They set up the expectation that carnivore-formed assemblages are roughly attritional (old-dominated) because young animals are thoroughly consumed by carnivores, while hominin assemblages are broadly catastrophic (high percentages of young and prime-aged adults) (Klein et al. 2007, 180-182). They establish that cape buffalo conforms to an attritional mortality profile, which supports their interpretation that carnivores were responsible for the assemblage. The zebra profile is catastrophic, but instead of attributing this to hominin hunting efforts, they propose that it reflects the formation environment of the assemblage along a shallow lakeshore or in marshlands (Klein et al. 2007, 183). It is also worth noting that Gaudzinski (2004) observed an identical (0.2 %) cut mark percentage at 'Ubeidiya, which contributed to her interpretation that certain taxa were probably hunted by hominins 1.4 Ma. This case study highlights the often subjective nature of interpreting the taphonomic record, and that there is still a long way to go before zooarchaeologists agree on the best way to apply mortality data.

In Eurasia, sites are regularly interpreted as providing convincing evidence that hominins had entered the hunting niche after 1.0 Ma. Much of the information we have about this period comes from southern Europe. Martinez et al. (2010) postulate that hominins were predators at 830,000 BP at Vallparadís in southern Spain. This is based on the diversity of taxa found at the site, as well as the represented elements and the mortality data, but the authors provide few details. Sierra de Atapuerca in northern Spain preserves a long sequence of hominin activity and subsistence data. Layer TDW4 at Gran Dolina (Atapuerca) is undated, but lies below 857,000-780,000 year-old deposits. Due to the location and kinds of butchery damage on the faunas, Huguet et al. (2013) concludes that hominins had primary access to the bones, which they interpret as hunting or confrontational scavenging by hominins. Multiple analysts have examined the faunal assemblages from layer TD6.2, also at Gran Dolina, which yields a date of at least 780,000 BP. Saladié et al. (2011) provide the most complete and updated presentation of the faunas (but see Diez et al. 1999 for an earlier version, and Huguet et al. 2013 for an additional summary). The faunal spectrum is fairly diverse, but skews to mammals in the 100-300 kg range. The assemblage is comprised primarily of limb and head elements, which the authors interpret as hominins mostly transporting carcasses to the site complete, then carnivores ravaging the more fragile axial elements (Saladié et al. 2011). Cut marks are common, and in instances where cut marks and carnivore gnaw marks are found on the same specimen, tooth marks are always on top of cuts, indicating hominins had primary access to the remains. Based on taphonomic damage and anatomical profiles, Saladié et al. (2011) postulate that groups of hominins hunted ungulates, then delayed consumption of animal tissues in order to carry meat back to the base camp to share with others in the group. The authors publish mortality profile data, and conclude that immature and adult animals dominate the assemblages. The methods divide ungulate ages into four different groups as opposed to other commonly used schemes that use three divisions (e. g. Stiner 1990; 2005; Steele / Weaver 2002; Weaver / Boyko / Steele 2011; Discamps / Costamagno 2015), and when their data are adjusted and plotted on a tripolar graph, a fairly clear prime-aged adult bias emerges, which many faunal specialists interpret as evidence for hominin hunting behaviors.

Moving to Israel, Gesher Benot Ya'aqov (MIS 20-18, ca. 815,000-710,000 BP) preserves a rich faunal spectrum along the edge of a paleolake (Rabinovich et al. 2008; Rabinovich / Biton 2011). Though the authors have identified a range of cervids, bovids, and megafauna, the most notable remains are those of fallow deer. Rabinovich / Gaudzinski-Windheuser / Goren-Inbar (2008) document repetitive butchery marks on at least ten individuals, which leads them to conclude that hominin hunters at the site understood prey anatomy, and also had the technical and communication skills necessary to process the carcasses in a standardized way.

The next available faunal assemblages date to more than 100,000 years later than Gesher Benot Ya'aqov. Caune de l'Arago Cave (France) contains at least four major archaeological deposits that span from 550,000 to 440,000 BP (Moigne / Barsky 1999; Rivals / Kacimi / Moutoussamy 2004). Depending on the layer, a different ungulate taxon dominates (reindeer, red and fallow deer, musk ox, and argali, from oldest to youngest layers), but in all cases adults are well-represented in the assemblages (Moigne / Barsky 1999; Rivals / Kacimi / Moutoussamy 2004).

Both sets of authors hypothesize that these heavily-butchered faunas were formed by hominin hunting practices, but Rivals/Kacimi/Moutoussamy (2004) present reconstructions of sex ratios and seasonality for all of the layers and conclude that hominins were following a non-selective hunting strategy, exploiting the most commonly available animals of a particular taxa in each time period.

In Great Britain, Boxgrove (MIS 13-12, ca. 490,000 to 425,000 BP) has cut bones in multiple archaeological layers from different ungulate taxa, especially cervids and horse, but also on some megafauna (Smith 2012; 2013). Most notable is a butchered horse (*Equus ferus*) individual with evidence of an impact mark on the scapula, which might have come from a wooden spear similar to those found at Schöningen (Roberts/Parfitt 1999; Smith 2012; 2013). The excavators and analysts interpret the remains as evidence for primary access through hominin hunting or confrontational scavenging, but do not specify which is more likely. Also in Great Britain, fauna found in association with lithics and fossil hominin remains at Swanscombe played an important part in the hunting versus scavenging debate of the 1960s-1980s. On the one hand, the excavator, John d'Arcy Waechter (1968; 1969; 1976), claimed that the site was evidence of a riverside hunting camp, while Binford (1985) argued that it actually represents hominin scavenging behaviors. In a recent reanalysis of the materials, Smith (2012; 2013) concludes that a combination of taphonomic factors and excavation methods actually does not leave enough evidence to support either claim, which is largely similar to the situation with Torralba and Ambrona that we discussed above.

Returning to the later layers at Sierra de Atapuerca in Spain, Galería preserves several archaeological layers, including GII and GIIIa, which date to roughly 500,000-460,000 BP. During this phase, the site was a natural trap for juvenile ungulates, which were subsequently scavenged by both hominins and carnivores (Huguet Pamies et al. 2001; Rodríguez et al. 2011). The authors hypothesize that hominins had access to carcasses before carnivores, and note that long bones were selectively transported away from the cave. Layer TD10.2 at Gran Dolina contains some of the most compelling early evidence for large game hunting we have presented so far. The deposit contains at least 60 individual bison carcasses that were heavily processed by hominins (Rodríguez-Hidalgo et al. n.d.). Rodríguez-Hidalgo et al. (n.d.) note the large number of axial elements in the assemblage, which leads them to conclude that the animals died at the site. Ageing data reflects a catastrophic mortality profile, and microwear analyses of the teeth indicates that the animals died in at least two seasons (late spring and early fall) (Rodríguez-Hidalgo et al. 2016; n.d.). Based on these multiple lines of evidence, the authors make the case that hominins engaged in communal hunting on more than one occasion, by using the contours of the cave as a natural trap for bison. This would have required an advanced level of planning, communication, and technological investment, which shows a fairly high level of cognition for late Lower Paleolithic hominins at Gran Dolina (Rodríguez-Hidalgo et al. n.d.).

Stopp (1993) presents the faunal remains from Hoxne in Great Britain, which was recently dated to MIS 11 (ca. 424,000-374,000 BP) (Ashton et al. 2008). The assemblage is not large, and while the author hypothesizes that hominins preferred horse (*Equus ferus*) and red deer at the site, it is impossible to determine whether hunting or scavenging was the method of meat acquisition (Stopp 1993). The faunal assemblage from Qesem Cave (400,000-200,000 BP) in Israel is much larger and has been studied in greater detail. Stiner and colleagues (2009; Stiner/Barkai/Gopher 2011) present a sample identified from multiple layers in the site. They make a strong case that hominins using the cave were hunting, in particular medium to large bodied ungulates, then were preferentially transporting meat- and marrow-rich elements to the site in order to share with other members of the group. They also use mortality profiles to establish that hominins were intentionally targeting prime-aged adult ungulates, in this case fallow deer, which is consistent with the hunting niche we see later among Middle and Upper Paleolithic hominins (Stiner/Barkai/Gopher 2009; 2011). In a later study, Blasco and colleagues (2014) present a more focused analysis of a single hearth area at Qesem. The fauna from the hearth largely agrees with Stiner's studies, with a dominance of fallow deer and a large number of high-utility elements that were probably shared with a larger group. However, the authors seem to find a slightly wider mortality profile for fallow deer, which they interpret to reflect cooperative hunting, possibly of multiple animals at once. We should note that their age categories conform to those used by Saladié et al. (2011), and are not consistent with those found in earlier studies of Qesem (Stiner/Barkai/Gopher 2009; 2011). If we apply the conventions set forth by Stiner, Steele, and Weaver (Stiner 1990; 2005; Steele/Weaver 2002; Weaver/Boyko/Steele 2011), the hearth area at Qesem does not differ from the larger sample. Despite this difference in analytical techniques, Blasco and colleagues (2014) note the threads of modernity that seem to emerge during this period at Qesem, at least in terms of cooperative hunting and meat sharing, which we also find in common with Late Pleistocene hominins.

We now move to the latest set of sites in this review, which were formed in the warm interglacial of MIS 9. Level 6 at Orgnac 3 (France) dates to about 300,000 BP (Moigne/Barsky 1999; Moncel/Moigne/Combier 2005). The cave contains heavily butchered cervid, bovid, horse, and pig bones, many of which were brought to the site complete. The authors note repetitive fracture patterns, particularly on horse long bones, which they interpret as more organized butchery than what is typically seen at older sites (Moigne/Barsky 1999; Moncel/Moigne/Combier 2005). Blasco and colleagues (2013) present faunal data from the 300,000 year old layer TD10-1 at Gran Dolina and similarly-dated levels at Bolmor Cave (Spain). In addition to highlighting some incidences of small game use (see above), the authors mainly find that hominins exploited a wide range of taxa in these particularly diverse environments. In a more detailed look at the TD10-1 Gran Dolina assemblage, Rodríguez-Hidalgo et al. (2015) make the case that during this period the site was used as a hominin base camp. They note a dominance of red deer, which they attribute to selective hunting. The authors record ample evidence of butchery, and note that carcass transport patterns seem to indicate a preference for marrow-rich elements. Mortality data from the site indicate a preference for prime-aged adult animals, so the authors conclude that occupants of the site had entered into the hominin prey niche (Rodríguez-Hidalgo et al. 2015). We should note that the authors used the tripolar age grouping model, as opposed to dividing animals into four cohorts.

Our final example is Schöningen (Germany, 300,000 BP), which also contains strong evidence for hunting. The site is situated alongside a paleolake and preserves the remains of over fifty horses, in addition to nine wooden spears, which if interpreted correctly, represent the earliest hunting implements recorded to date (Thieme 1997; Voormolen 2008; Conard et al. 2015b). The faunas are overwhelmingly comprised of large-bodied Pleistocene horses (*Equus mosbachensis*) with extensive evidence of meat removal and marrow extraction (Voormolen 2008; Van Kolfschoten 2014; Starkovich/Conard 2015; Van Kolfschoten/Buhrs/Verheijen 2015). Body part profiles are largely complete, indicating that the animals died at or near the site (Voormolen 2008; Starkovich/Conard 2015). Mortality data conform to a catastrophic age profile, with a large number of prime adult and juvenile animals in the death assemblage (Voormolen 2008). Originally, when Schöningen was first excavated, archaeologists interpreted it as a mass kill (e. g. Thieme 2000; 2005; 2007). However, with further analysis of the faunal remains and isotopes, multiple lines of evidence point to a number of kill events of one or many animals at a time, along with the accumulation of a few individuals that died naturally (Musil 2007; Voormolen 2008; Julien et al. 2015; Kuitems et al. 2015, but see Van Kolfschoten 2014 for an argument favoring one large event along with the background accumulation of many animals). Regardless of the exact formation processes of the site, the combination of mortality profiles, a large number of heavily processed horse carcasses, and wooden spears leads to a compelling argument for hominin hunting at Schöningen.

After 1.0 Ma, the evidence for hominin hunting, and certainly primary access to meat during scavenging situations, seems to be more solid. Samples from this period tend to be overall larger and more numerous than before 1.0 Ma, so archaeologists are able to apply a greater range of analytical techniques to available datasets in order to more securely interpret hominin behaviors. In addition, there are a few instances of more direct evidence for hominin hunting: the impact fracture on the horse scapula at Boxgrove (Roberts/Parfitt 1999; Smith 2012; 2013), the apparent communal hunting of bison at Gran Dolina (Rodríguez-Hidalgo et al. 2016; n. d.), and the dozens of horses found associated with wooden spears at Schöningen (Thieme 1997; Voormolen 2008; Conard et al. 2015b). It is worth noting that there seems to be a fundamental difference, not just in the archaeological data, but also the interpretive framework many analysts use when trying to understand their results from this period. With the exception of a few authors (e. g. Huguet Pamies et al. 2001; Echassoux 2004; Gaudzinski 2004; Bunn/Pickering 2010; Bunn/Gurtov 2014), most zooarchaeologists working on sites that date to before 1.0 Ma do not explicitly state that hunting by hominins was a possible route to meat acquisition. Yet after this time, Klein and colleagues (2007) stand out as the lone voices that deny hunting as a possibility. Perhaps the line is more appropriately drawn between Eurasian and African sites regardless of their chronology; analysts working in Europe are much quicker to propose hunting, while those studying African sites hedge on this issue, almost as if it is natural to assume that hominins that are capable of leaving Africa were also advanced enough to hunt large-bodied game. Whatever the explanation, these *a priori* assumptions seem to color the conclusions drawn by faunal analysts. In several cases, which we highlighted above, nearly identical evidence from sites in different regions or times is used to argue completely opposite positions. For this reason, in addition to using multiple lines of consistent evidence for identifying hominin hunting or primary meat acquisition, it would be useful for faunal analysts to at least adopt a consistent null hypothesis when approaching Lower Paleolithic zooarchaeological assemblages. The most prudent starting point for analysts, given the evolutionary history of hominins before the advent of stone tools, is to assume that Lower Paleolithic hominins were *not* actively involved in large game procurement. This should ensure that arguments to the contrary are supported by convincing data, which is certainly the case with many (but not all) examples cited above, and would help us better understand the appearance and importance of early hunting and active scavenging behaviors.

Impacts on carnivore communities

Throughout this paper carnivores have played a consistent, though somewhat periphery, role in our discussion. At the oldest sites, carnivores are important because hominins might have directly competed with them for carcasses, or even capitalized on their hunting efforts through kleptoparasitism (meat theft). It is interesting to consider the effect this might have had on the evolutionary success of top predators. Many authors have investigated this question through studies of carnivore behavior, migrations, and the modelling of carnivore niches (Turner 1988; Marean 1989; Lewis 1997; Werdelin/Lewis 2005; 2013; Croitor/Brugal 2010; Rodríguez et al. 2012), and it seems plausible that hominins had an impact on the predator guild not long after they regularly began to incorporate meat into their diets.

Along these lines, one question that has surfaced in the literature is whether or not hominins targeted specific predators from which to scavenge, for example cheetahs (*Acinonyx pardinensis*) or certain species of sabertooth cat (e. g. *Megantereon*) (Lewis/Werdelin 2010; Hemmer/Kahlke/Vekua 2011). Hemmer/Kahlke/Vekua (2011) present carnivore remains from Dmanisi and point out that a single adult cheetah has about 1,000 kg of meat per year stolen by other carnivores, which might have been a significant food source for early hominins. Similarly, Lewis and Werdelin (2010) explore the hypothesis that East African Plio-Pleistocene hominins specifically targeted the sabertooth *Megantereon* for scavenging opportunities. However, they note that this kind of dynamic would have exerted a negative selective pressure on the sabertooth. Not only is there no evidence for this, but both *Megantereon* and hominins left Africa at roughly the same time and continued to co-exist for many millennia afterwards. They hypothesize that after 1.8 Ma, hominins started to become a significant part of the ecosystem as scavenging meat-eaters. This shift likely destabilized the entire carnivore guild, though it was not extreme enough to cause the extinction of the many carnivore taxa that disappear at this time (Lewis/Werdelin 2010).

In a discussion of changes in the broader African carnivore guild, Werdelin and Lewis (2013) model the functional richness and evenness of the ecosystem between 3.5 and 1.5 Ma. The authors find that there was a depression in both the number of large-bodied carnivores, and a reduction in overall niche width after 2.0 Ma, which is about the same time we start to see multiple examples of hominin meat acquisition. Even more compelling, the first clear decline appears among large African omnivores at 2.0 Ma, which likely would have been the first group of species impacted by largely herbivorous hominins starting to eat meat. This is followed by a decrease in canids and hypercarnivorous felids (i. e., animals whose diets include more than 70 % meat, see Holliday/Steppan 2004) by 1.5 Ma. Werdelin and Lewis (2013) are quick to point out that a climatic explanation might also exist, particularly for the disappearance of omnivorous taxa, though this is probably not the case for hypercarnivores, and concludes that one possible cause of this change to the carnivore guild was the appearance of more meat-reliant hominins after 2.0 Ma.

Egeland (2014) examines this question from a different angle, by looking specifically at carnivore-hominin competition at several localities at Olduvai Gorge Beds I and II. He points out that sites with evidence for exploitation by both carnivores and hominins must have formed fairly quickly since carcasses are only edible for a finite amount of time, particularly in hot climates. This is directly related to competition because it addresses the degree of avoidance between early hominins and carnivores. In the study, Egeland (2014) conducts a multivariate analysis based on lithic densities and butchered bones at some of the Bed I and II sites. He finds no negative correlation between carnivore intensity and hominin behavior, and in fact at Bed II there is an increase in lithic densities when carnivore activities intensify. This leads him to conclude that even by 1.4 Ma, hominins were not intentionally avoiding places on the landscape where carnivores were active, and were instead successfully competing with carnivores for space and resources (Egeland 2014). He proposes some possible reasons for this success, such as changes in body size, group size, or technological factors (e. g. spears, fire, etc.), though he does not speculate as to which factor was the cause. Egeland (2014) also cites work by Werdelin and Lewis (2005), who place the extinction of multiple species of sabertooth hypercarnivores at about the same time.

Croitor and Brugal (2010) explore similar questions regarding carnivore guild dynamics in the Plio-Pleistocene of Eurasia. At 1.8 Ma, several significant taxa including *Homo* entered Eurasia, along with the relatively flexible or social carnivores: jaguar (*Panthera onca*), hunting dog (*Lykaon*), and giant hyena (*Pachycrocuta brevirostris*). After this time, and especially after 1.0 Ma, many of the solitary hypercarnivores (mostly felids) went extinct and social hunters (e. g. lions, striped hyenas, wolves) and omnivores expanded (Croitor/Brugal 2010). The authors compare this to similar changes in East Africa, specifically the decline of specialist carnivores and corresponding expansion of generalist carnivores (canids and *Panthera* sp.) (Werdelin/Lewis 2005). Croiter and Brugal (2010) hypothesize that this benefitted hominins who entered Eurasia into an impoverished predator guild.

Looking at southern Europe, Rodríguez et al. (2012) reconstruct the predator guild between 2.6 and 0.78 Ma. They find relatively low levels of carnivore competition in early and later phases of their study, but an extremely competitive situation shortly before 1.2 Ma, which either coincides with or slightly postdates the earliest arrival of hominins. The authors take the position that hominins probably entered southern Europe early enough that the carnivore guild was still quite competitive. Based on this, Rodríguez et al. (2012) conclude that early hominins in Europe were most likely flexible feeders, a position that supports the model proposed by Ungar / Grine / Teaford (2006) that attributes the overall success of hominins to flexible omnivory. However, Rodríguez et al. (2012) also note that a large number of scholars interpret the decline of carnivores and appearance of hominins in southern Europe as related phenomena (e.g. Turner 1992; Martinez-Navarro / Palmqvist 1996; Arribas / Palmqvist 1999; Palombo 2010).

In general, it is difficult to determine the cause-and-effect nature of the evolutionary pressures between carnivores and hominins in the Plio-Pleistocene because the temporal resolution is so poor. However, the carnivore-based studies we reviewed above indicate that hominins might have begun to impact certain predator communities between 2.0 and 1.5 Ma. This is interesting, as it corresponds well with the earliest relatively widespread evidence for meat eating by hominins. This also suggests that by the time hominins entered Eurasia, they were already engaged in some degree of competition with carnivores. A particularly striking line of evidence regarding carnivore-hominin competition regards situations where cut marks and bite marks overlap on a single faunal specimen. Though this is rare, it occurs at enough sites and typically seems to follow the same pattern that it is important. Starting at sites dating to 1.8 Ma, there are multiple examples of carnivore bite marks overlying cut marks from hominin stone tools. Analysts have observed this at El-Kherba (1.8 Ma; Sahnouni et al. 2013), Dmanisi (1.77 Ma; Lordkipanidze et al. 2007), Gran Dolina (ca. 800,000 BP; Blasco / Rosell 2009; Rodríguez et al. 2011), Boxgrove (490,000-425,000 BP; Smith 2012; 2013), and Schöningen (300,000 BP; Voormolen 2008; Starkovich / Conard 2015, but see Van Kolfschoten 2015 for one or two examples of cut marks on top of bites). We can only explain these observations if 1) carnivores actively chased hominins off of carcasses, or hominins were concerned about this threat, or 2) carnivores had secondary access to animal remains after hominins were done. Based on multiple lines of evidence we have presented in this paper we argue that the latter is the case. Within this discussion it is important to keep in mind that even if hominins on the species- or population-level gained primary access to meat or entered the carnivore guild between 2.0 and 1.5 Ma, encounters between individual hominins and carnivores probably did not always favor the hominin. Furthermore, it is likely that early hominins and carnivores avoided each other, at least in the sense that the two groups did not seek one another out to initiate conflicts.

Discussion and Conclusions

The timing and nature of the origins of meat acquisition by hominins are among the most important and difficult questions in understanding human evolution. Access to a wider range of protein and other nutrients certainly had an effect on the cognitive capabilities of early hominins, but it was also critical from a co-evolutionary point of view in terms of the competitive challenges between hominins and carnivores. Based on the evidence we have reviewed here, it is difficult to pinpoint an exact date for the origins of meat acquisition in general, or hunting behaviors in particular, and in fact such a conclusion would oversimplify the actual situation. One reason for this is that the incorporation of meat into the diet was not a one-time event that catalyzed a universal shift to meat eating. Dietary flexibility is one of the most successful adaptations of the hominin lineage (e.g. Ungar / Grine / Teaford 2006), so there is no reason to believe that once meat-eating began it was adopted uniformly between or even within populations. The second reason is that meat acquisition for many carnivores exist along a continuum between hunting and scavenging, and omnivorous hominins are no different. Since we know that modern hunter-gatherers regularly subsist on some percentage of scavenged meat (e.g.

O'Connell/Hawkes/Jones 1988; Bunn 2001) despite having the tools and skill to shift completely to a hunting-based diet, there is little reason to believe that any past hominin groups acquired meat entirely through hunting. We also cannot forget that some of our closest primate relatives occasionally eat meat without the aid of stone tools, so it is possible that meat-eating actually has its origins in a form unrecognizable in the archaeological record before ape and hominin lineages even split. This hypothesis is difficult to test, though most of the meat-eating we focus on in this paper involves the consumption of large animals (relative to hominin body size), which is not found among monkeys and the great apes, so it is likely that this behavioral pattern appeared later. Despite these many difficulties, we do see some trends in the literature that allow us to draw some conclusions regarding the origins of meat eating by hominins.

First, evidence from Gona, Omo, and Dikika indicate that hominins had occasional access to meat (and fish) before 2.0 Ma. This is important for marking some of the earliest meat eating, though it does not seem to represent a fundamental or universal shift in subsistence strategies to regular carnivory. An increase in evidence for meat eating, including aquatic resource exploitation, scavenging, and possible occasional hunting of large terrestrial mammals, appears in both Africa and Eurasia between 1.8 and 1.5 Ma. This begs the question of whether hominins started exploiting meat on a more regular basis before or after they left Africa, which unfortunately we cannot address with the current state of the data. It is also significant that there was a fairly substantial change in the carnivore guilds of Africa and Eurasia at about the same time. This is reflected in the localized extinction of certain taxa (e. g. sabertooth cats), but also broader behavioral groups of carnivores (e. g. some omnivores and specialized hypercarnivores). Due to the temporal resolution of the sites from this period, it is unclear if the entrance of hominins into the carnivore guild drove some or all of these processes, or if the natural evolution of the guild left a niche open for omnivorous hominins. There is compelling evidence that hominins were able to compete on a fairly high level with other carnivores even at this early stage, for example carnivore bite marks found on top of cut marks at multiple sites starting at 1.8 Ma, or Egeland's (2014) conclusions that intense carnivore competition had little effect on hominin activities at 1.4 Ma at Olduvai Gorge Beds I and II.

The second conclusion we draw is that the evidence for hominin hunting after 500,000 BP is clear. This is particularly the case in Eurasia where most sites dating to this time period are located, but there is no reason to believe that hominin hunting was also not well-developed in Africa at the same time. It is possible, or even likely, that there is earlier evidence for hunting, perhaps at ca. 800,000 BP (e. g. Vallparadís or Gran Dolina TD6.2) or even at 1.75 Ma (FLK Zinj), but after 500,000 BP sites such as Gran Dolina TD10.2, Boxgrove, and Schöningen provide irrefutable evidence.

As a side point that has less to do with the archaeological record, we notice some difficulties in comparing data between the sites, as well as some interesting differences in the null hypotheses and interpretations of faunal analysts working in different time periods and geographic regions. To the first issue, different methods in terms of data collection and interpretation are definitely not unique to Lower Paleolithic zooarchaeology, nor is there an obvious solution to this problem. However, it does seem that the highest profile debates on this topic (i. e., primary meat acquisition at Olduvai Gorge) center around different scholars approaching the exact same assemblages differently by highlighting one or two lines of evidence (e. g. location of cut marks, location of bite marks, species representation, etc.), and authors who take into account as much of these kinds of data as possible are able to support their arguments more convincingly. We agree with many other authors (e. g. Klein 1981; 1982; Klein/Allwarden/Wolf 1983; Klein/Cruz-Uribe 1984; Stiner 1990; 2002; 2005; Bunn/Pickering 2010; Bunn/Gurtov 2014) that establishing mortality profiles for prey taxa in archaeological assemblages is critical to attempting to understand if faunas were formed by carnivores or hominins.

And while the tripolar system established by Stiner (1990; 2005) is extremely popular, revisions by Weaver, Steele, and colleagues (2002; 2011), and more recently Discamps (2015) provide mathematically based updates to the model that highlight the importance of understanding the herd structure of individual taxa (see also Kahlke / Gaudzinski 2005; Stiner 2005 for more examples of this). Therefore, analyses of Lower Paleolithic assemblages should ideally include species abundance, butchery, fragmentation, carnivore, and mortality data whenever possible, as well as isotope and tooth meso- and micro-wear analyses.

To the second issue, it would be beneficial if faunal analysts studying the Lower Paleolithic could at minimum agree on a null hypothesis. Since one of the main goals of this period is to establish the origins of hominin meat acquisition or hunting, it seems that the burden of proof should be on the side arguing that hominins were established hunters. This seems like a pragmatic solution until we have a larger set of data from this time period, and indeed this approach is the already-established pattern, particularly among archaeologists working in Africa or on pre-1.0 Ma sites.

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References

Adler et al. 2006: D. S. Adler / G. Bar-Oz / A. Belfer-Cohen / O. Bar-Yosef, Ahead of the Game: Middle and Upper Palaeolithic Hunting Behaviors in the Southern Caucasus. Current Anthropology 47, 2006, 89-118.

Anzidei / Cerilli 2001: A. P. Anzidei / E. Cerilli, The fauna of La Polledrara di Cecanibbio and Rebibbia-Casal de' Pazzi (Rome, Italy) as an indicator for site formation processes in a fluvial environment. In: G. Cavarretta / P. Gioia / M. Mussi / M. R. Palombo (eds.), Proceedings of the 1st International Congress the World of Elephants. CNR (Rome 2001) 167-171.

Anzidei et al. 2012: A. P. Anzidei / G. M. Bulgarelli / P. Catalano / E. Cerilli / R. Gallotti / C. Lemorini / S. Milli / M. R. Palombo / W. Pantano / E. Santucci, Ongoing research at the late Middle Pleistocene site of La Polledrara di Cecanibbio (central Italy), with emphasis on human-elephant relationships. Quaternary International 255, 2012, 171-187.

Archer / Braun 2013: W. Archer / D. R. Braun, Investigating the signature of aquatic resource use within Pleistocene hominin dietary adaptations. PLOS ONE 8, 2013, e69899.

Archer et al. 2014: W. Archer / D. R. Braun / J. W. K. Harris / J. T. McCoy / B. G. Richmond, Early Pleistocene aquatic resource use in the Turkana Basin. Journal of Human Evolution 77, 2014, 74-87.

Arribas / Palmqvist 1999: A. Arribas / P. Palmqvist, 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. Journal of Archaeological Science 26, 1999, 571-585.

Ashton et al. 2008: N. Ashton / S. G. Lewis / S. A. Parfitt / K. E. H. Penkman / G. Russell Coope, New evidence for complex climate change in MIS 11 from Hoxne, Suffolk, UK. Quaternary Science Reviews 27, 2008, 652-668.

Berthelet / Chavaillon 2001: A. Berthelet / J. Chavaillon, The Early Palaeolithic butchery sites of Barogali (Republik of Djibouti). In: G. Cavarretta / P. Gioia / M. Mussi / M. R. Palombo (eds.), The World of Elephants. Proceedings of the First International Congress. CNR (Rome 2001) 176-179.

Binford 1981: L. R. Binford, Bones: Ancient Men and Modern Myths (New York 1981).

1985: L. R. Binford, Human Ancestors: Changing Views of Their Behavior. Journal of Anthropological Archaeology 4, 1985, 292-327.

1987: L. R. Binford, Were there elephant hunters at Torralba? In: M. H. Nitecki / D. Nitecki (eds.), The Evolution of Human Hunting (New York 1987) 47-105.

1988: L. R. Binford, The hunting hypothesis, archaeological methods and the past. Yearbook of Physical Anthropology 30, 1988, 1-9.

Binford/Bertram 1977: L. R. Binford / J. B. Bertram, Bone Frequencies – And Attritional Processes. In: L. R. Binford (ed.), For Theory Building in Archaeology (New York 1977) 77-156.

Binford/Blumenschine 1986: L. R. Binford / R. J. Blumenschine, Response to Bunn and Kroll. Current Anthropology 27, 1986, 444-446.

Blasco/Peris 2009: R. Blasco / J. F. Peris, Middle Pleistocene bird consumption at Level XI of Bolomor Cave (Valencia, Spain). Journal of Archaeological Science 36, 2009, 2213-2223.

2012: R. Blasco / J. F. Peris, A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave. Quaternary International 252, 2012, 16-31.

Blasco/Rosell 2009: R. Blasco / J. Rosell, Who was the first? An experimental application of carnivore and hominid overlapping marks at the Pleistocene archaeological sites. Comptes Rendus – Palevol 8, 2009, 579-592.

Blasco et al. 2011: R. Blasco / H.-A. Blain / J. Rosell / J. Carlos Díez / R. Huguet / J. Rodríguez / J. L. Arsuaga / J. M. Bermúdez de Castro / E. Carbonell, Earliest evidence for human consumption of tortoises in the European Early Pleistocene from Sima del Elefante, Sierra de Atapuerca, Spain. Journal of Human Evolution 61, 2011, 503-509.

2013: R. Blasco / J. Rosell / J. F. Peris / J. L. Arsuaga / J. M. Bermúdez de Castro / E. Carbonell, Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). Quaternary Science Reviews 70, 2013, 124-144.

2014: R. Blasco / J. Rosell / A. Gopher / R. Barkai, Subsistence economy and social life: A zooarchaeological view from the 300kya central hearth at Qesem Cave, Israel. Journal of Anthropological Archaeology 35, 2014, 248-268.

Blumenschine 1986: R. J. Blumenschine, Early hominid scavenging opportunities: implications of carcass availability in the Serengeti and Ngorongoro ecosystems. British Archaeological Reports International Series 283 (Oxford 1986).

1988: R. J. Blumenschine, An Experimental Model of the Timing of Hominid and Carnivore Influence on Archaeological Bone Assemblages. Journal of Archaeological Science 15, 1988, 483-502.

1991: R. J. Blumenschine, Hominid carnivory and foraging strategies, and the socio-economic function of early archaeological sites. Philosophical Transactions of the Royal Society A 334, 1991, 211-221.

1995: R. J. Blumenschine, Percussion marks, tool marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. Journal of Human Evolution 29, 1995, 21-51.

Blumenschine/Marean 1993: R. J. Blumenschine / C. W. Marean, A carnivore's view of archaeological bone assemblages. In: J. Hudson (ed.), From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains. Center for Archaeological Investigations, Southern Illinois University (Carbondale 1993) 273-300.

C. Boesch/H. Boesch 1989: C. Boesch / H. Boesch, Hunting behavior of wild chimpanzees in the Tai National Park. American Journal of Physical Anthropology 78, 1989, 547-573.

Boschian/Saccà 2010: G. Boschian / D. Saccà, Ambiguities in human and elephant interactions? Stories of bones, sand and water from Castel di Guido (Italy). Quaternary International 214, 2010, 3-16.

Bramble/Lieberman 2004: D. M. Bramble / D. E. Lieberman, Endurance running and the evolution of *Homo*. Nature 432, 2004, 345-352.

Braun et al. 2010: D. R. Braun / J. W. K. Harris / N. E. Levin / J. T. McCoy / A. I. R. Herries / M. K. Bamford / L. C. Bishop / B. G. Richmond / M. Kibunjia, Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. Proceedings of the National Academy of Sciences USA 107, 2010, 10002-10007.

Broadhurst/Cunnane/Crawford 1998: C. L. Broadhurst / S. C. Cunnane / M. Crawford, Rift Valley lake fish and shellfish provided brain-specific nutrition for early *Homo*. The British Journal of Nutrition 79, 1998, 3-21.

Bunn 1983: H. T. Bunn, Evidence on the diet and subsistence patterns of Plio-Pleistocene hominids at Koobi Fora, Kenya, and at Olduvai Gorge, Tanzania. In: J. Clutton-Brock / C. Grigson (eds.), Animals and Archaeology: 1. Hunters and Their Prey. British Archaeological Reports International Series 163 (Oxford 1983) 21-30.

1991: H. T. Bunn, A taphonomic perspective on the archaeology of human origins. Annual Review of Anthropology 20, 1991, 433-467.

1997: H. T. Bunn, The bone assemblages from the excavated sites. In: G. Isaac / B. Isaac (eds.), Koobi Fora Research Project. Plio-Pleistocene Archaeology Vol. 5 (Oxford 1997) 402-444.

2001: H. T. Bunn, Hunting, power scavenging, and butchering by Hadza foragers and by Plio-Pleistocene Homo. In: C. B. Stanford / H. T. Bunn (eds.), Meat-Eating and Human Evolution (New York 2001) 199-218.

2007: H. T. Bunn, Meat Made us Human. In: Evolution of the Human Diet: The Known, the Unknown, and the Unknowable (Oxford 2007) 191-211.

Bunn/Ezzo 1993: H. T. Bunn / J. A. Ezzo, Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. Journal of Archaeological Science 20, 1993, 365-398.

Bunn/Gurtov 2014: H. T. Bunn / A. N. Gurtov, Prey mortality profiles indicate that Early Pleistocene *Homo* at Olduvai was an ambush predator. Quaternary International 322-323, 2014, 44-53.

Bunn/Kroll 1986: H. T. Bunn / E. M. Kroll, Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania. Current Anthropology 27, 1986, 431-452.

Bunn/Pickering 2010: H. T. Bunn / T. R. Pickering, Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running–hunting and passive scavenging by early Pleistocene hominins. Quaternary Research 74, 2010, 395-404.

Bunn/Bartram/Kroll 1988: H. T. Bunn / L. E. Bartram Jr. / E. M. Kroll / Variability in Bone Assemblage Formation from Hadza Hunting, Scavenging, and Carcass Processing. Journal of Anthropological Archaeology 7, 1988, 412-457.

Bunn et al. 1980: H. T. Bunn / J. W. K. Harris / G. Isaac / Z. Kaufulu / E. M. Kroll / K. Schick / N. Toth / A. K. Behrensmeyer, FxJj50: an Early Pleistocene Site in Northern Kenya. World Archaeology 12, 1980, 109-136.

Capaldo 1997: S. D. Capaldo, Experimental determination of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (*Zinjanthropus*), Olduvai Gorge, Tanzania. Journal of Human Evolution 33, 1997, 555-597.

1998a: S. D. Capaldo, Methods, marks, and models for inferring hominid and carnivore behavior. Journal of Human Evolution 35, 1998, 323-326.

1998b: S. D. Capaldo, Simulating the Formation of Dual-Patterned Archaeofaunal Assemblages with Experimental Control Samples. Journal of Archaeological Science 25, 1998, 311-330.

Cassoli et al. 1999: P. F. Cassoli / G. Fabbo / I. Fiore / M. Piperno / A. Tagliacozzo, Taphonomic analysis of some levels of the Lower Palaeolithic site of Notachirico. In: S. Gaudzinski / E. Turner (eds.), The Role of Early Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages (Mainz 1999) 153-172.

Chavaillon 1976: J. Chavaillon. Evidence for the technical practices of Early Pleistocene hominids. In: Y. Coppens / F. C. Howell / G. L. Isaac / R. E. F. Leakey (eds.), Earliest Man and Environments in the Lake Rudolf Basin (Chicago 1976) 565-574.

Chavaillon et al. 1987: J. Chavaillon / J.-L. Boisaubert / M. Faure / C. Guérin / J. L. Ma / B. Nickel / G. Poupeau / P. Rey / S. A. Warsama, Le site de dépeçage pléistocène à Elephas recki de Barogali (République de Djibouti): nouveaux résultats et datation. C. R. Academy of Sciences Paris II 305, 1987, 1259-1266.

Conard et al. 2015a: N. J. Conard / C. E. Miller / J. Serangeli / T. Van Kolfschoten / M. F. Teaford (eds.), Excavations at Schöningen: New Insights into Middle Pleistocene Lifeways in Northern Europe. Journal of Human Evolution, Special Issue 89, 2015, 1-308

2015b: N. J. Conard / J. Serangeli / U. Böhner / B. M. Starkovich / C. E. Miller / B. Urban / T. van Kolfschoten, Excavations at Schöningen and paradigm shifts in human evolution. Journal of Human Evolution 89, 2015, 1-17.

Costamagno et al. 2006: S. Costamagno / L. Meignen / B. Cedric / B. Vandermeersch / M. Bruno, Les Pradelles (Marillac-le-Franc, France): A Mousterian reindeer hunting camp? Journal of Anthropological Archaeology 25, 2006, 466-484.

Croitor/Brugal 2010: R. Croitor / J.-P. Brugal, Ecological and evolutionary dynamics of the carnivore community in Europe during the last 3 million years. Quaternary International 212, 2010, 98-108.

de Heinzelin et al. 1999: J. de Heinzelin / J. D. D. Clark / T. D. T. White / W. K. W. Hart / P. Renne / Y. Beyene / E. Vrba / G. Woldegabrielt, Environment and behavior of 2.5-million-year-old Bouri hominids. Science 284, 1999, 625-635.

Diamond 1989: J. M. Diamond, Quaternary megafaunal extinctions: Variations on a theme by Paganini. Journal of Archaeological Science 16, 1989, 167-175.

Diez et al. 1999: J. C. Diez / Y. Fernández-Jalvo / J. Rosell / I. Caceres, Zooarchaeology and taphonomy of Aurora Stratum (Gran Dolina, Sierra de Atapuerca, Spain). Journal of Human Evolution 37, 1999, 623-652.

Discamps/Costamagno 2015: E. Discamps / S. Costamagno, Improving mortality profile analysis in zooarchaeology: A revised zoning for ternary diagrams. Journal of Archaeological Science 58, 2015, 62-76.

Domínguez-Rodrigo 1997: M. Domínguez-Rodrigo, Meat-eating by early hominids at the FLK 22 *Zinjanthropus* site, Olduvai Gorge, Tanzania: an experimental approach using cut mark data. Journal of Human Evolution 33, 1997, 669-690.

1999a: M. Domínguez-Rodrigo, Flesh availability and bone modification in carcasses consumed by lions. Palaeogeography, Palaeoclimatology, Palaeoecology 149, 1999, 373-388.

1999b: M. Domínguez-Rodrigo, Meat-eating and carcass procurement at the FLK Zinj 22 site, Olduvai Gorge (Tanzania): a new experimental approach to the old hunting-versus-scavenging debate. In: H. Ullrich (ed.), Lifestyles and Survival Strategies in Pliocene and Pleistocene Hominids (Schwelm 1999) 89-111.

2002: M. Domínguez-Rodrigo, Hunting and Scavenging by Early Humans: The State of the Debate. Journal of World Prehistory 16, 2002, 1-55.

Domínguez-Rodrigo/Pickering 2003: M. Domínguez-Rodrigo / T. R. Pickering, Early hominid hunting and scavenging: A zooarcheological review. Evolutionary Anthropology: Issues, News, and Reviews 12, 2003, 275-282.

Domínguez-Rodrigo/Bunn/Yravedra 2014: M. Domínguez-Rodrigo / H. T. Bunn / J. Yravedra, A critical re-evaluation of bone surface modification models for inferring fossil hominin and carnivore interactions through a multivariate approach: Application to the FLK Zinj archaeofaunal assemblage (Olduvai Gorge, Tanzania). Quaternary International 322-323, 2014, 32-43.

Domínguez-Rodrigo et al. 2002: M. Domínguez-Rodrigo / I. De La Torre / L. De Luque / L. Alcalá / R. Mora / J. Serrallonga / V. Medina, The ST Site Complex at Peninj, West Lake Natron, Tanzania: Implications for Early Hominid Behavioural Models. Journal of Archaeological Science 29, 2002, 639-665.

2009: M. Domínguez-Rodrigo / A. Mabulla / H. T. Bunn / R. Barba / F. Diez-Martín / C. P. Egeland / E. Espílez / A. Egeland / J. Yravedra / P. Sánchez, Unraveling hominin behavior at another anthropogenic site from Olduvai Gorge (Tanzania): new archaeological and taphonomic research at BK, Upper Bed II. Journal of Human Evolution 57, 2009, 260-283.

2010: M. Domínguez-Rodrigo / A. Z. P. Mabulla / H. T. Bunn / F. Diez-Martín / E. Baquedano / D. Barboni / R. Barba / S. Domínguez-Solera / P. Sánchez / G. M. Ashley / J. Yravedra, Disentangling hominin and carnivore activities near a spring at FLK North (Olduvai Gorge, Tanzania). Quaternary Research 74, 2010, 363-375.

2014a: M. Domínguez-Rodrigo / H. T. Bunn / A. Z. P. Mabulla / E. Baquedano / D. Uribelarrea / A. Pérez-González / A. Gidna / J. Yravedra / F. Diez-Martín / C. P. Egeland / R. Barba / M. C. Arriaza / E. Organista / M. Ansón, On meat eating and human evolution: A taphonomic analysis of BK4b (Upper Bed II, Olduvai Gorge, Tanzania), and its bearing on hominin megafaunal consumption. Quaternary International 322-323, 2014, 129-152.

2014b: M. Domínguez-Rodrigo / F. Diez-Martín / J. Yravedra / R. Barba / A. Mabulla / E. Baquedano / D. Uribelarrea /

P. Sanchez / M. I. Eren, Study of the SHK Main Site faunal assemblage, Olduvai Gorge, Tanzania: Implications for Bed II taphonomy, paleoecology, and hominin utilization of megafauna. Quaternary International 322-323, 2014, 153-166.

Eaton / Eaton III / Cordain 2002: S. B. Eaton / S. B. Eaton III / L. Cordain, Evolution, diet, and health. In: P. S. Ungar / M. F. Teaford (eds.), Human Diet: Its Origin and Evolution (Westport CT 2002) 7-18.

Echassoux 2004: A. Echassoux, Étude taphonomique, paléoécologique et archéozoologique des faunes de grands mammifères de la seconde moitié du Pléistocène inférieur de la grotte du Vallonnet (Roquebrune-Cap-Martin, Alpes-Maritimes, France). L'Anthropologie 108, 2004, 11-53.

Egeland 2014: C. P. Egeland, Taphonomic estimates of competition and the role of carnivore avoidance in hominin site use within the Early Pleistocene Olduvai Basin. Quaternary International 322-323, 2014, 95-106.

Egeland / Domínguez-Rodrigo 2008: C. P. Egeland / M. Domínguez-Rodrigo, Taphonomic perspectives on hominid site use and foraging strategies during Bed II times at Olduvai Gorge, Tanzania. Journal of Human Evolution 55, 2008, 1031-1052.

Espigares et al. 2013: M. P. Espigares / B. Martinez-Navarro / P. Palmqvist / S. Ros-Montoya / I. Toro / J. Agustí / R. Sala, *Homo vs. Pachycrocuta:* Earliest evidence of competition for an elephant carcass between scavengers at Fuente Nueva-3 (Orce, Spain). Quaternary International 295, 2013, 113-125.

Fernandez-Jalvo / Andrews / Denys 1999: Y. Fernandez-Jalvo / P. Andrews / C. Denys, Cut marks on small mammals at Olduvai Gorge Bed-I. Journal of Human Evolution 36, 1999, 587-589.

Fiore et al. 2004: I. Fiore / L. Bondioli / A. Coppa / R. Macchiarelli / R. Russom / H. Kashay / T. Solomon / L. Rook / Y. Libsekal, Taphonomic analysis of the Late Early Pleistocene bone remains from Buia (Dandiero Basin, Danakil depression, Eritrea): Evidence for large mammal and reptile butchering. Rivista Italiana di Paleontologia e Stratigrafia 110, 2004, 89-97.

Freeman Jr. 1978: L. G. Freeman Jr., Analysis of some occupation floor distributions from Earlier and Middle Paleolithic sites in Spain. In: L. G. Freeman Jr. (ed.), Views from the Past (The Hague, Paris 1978) 57-108.

Freeman Jr. / Butzer 1966: L. G. Freeman Jr. / K. W. Butzer, The Acheulian station of Torralba (Spain): a progress report. Quaternaria VIII, 1966, 9-22.

Freeman 1994: L. G. Freeman, Torralba and Ambrona: a review of discoveries. In: R. S. Corruccini / R. L. Ciochon (eds.), Integrative Paths to the Past (Engelwood Cliffs NJ 1994) 597-638.

Freeman / Freeman 1975: L. G. Freeman / L. G. Freeman Jr., Acheulian sites and stratigraphy in Iberia and the Maghreb. In: K. W. Butzer / G. L. Isaac (eds.), After the Australopithecines: Stratigraphy, Ecology and Culture Change in the Middle Pleistocene (The Hague, Paris 1975) 661-743.

Gaudzinski 1995: S. Gaudzinski, Wallertheim revisited: a re-analysis of the fauna from the Middle Palaeolithic site of Wallertheim (Rheinhessen / Germany). Journal of Archaeological Science 22, 1995, 51-66.

2004: S. Gaudzinski, Subsistence patterns of Early Pleistocene hominids in the Levant – taphonomic evidence from the 'Ubeidiya Formation (Israel). Journal of Archaeological Science 31, 2004, 65-75.

Gaudzinski / Roebroeks 2000: S. Gaudzinski / W. Roebroeks, Adults only: Reindeer hunting at the Middle Palaeolithic site Salzgitter Lebenstedt, northern Germany. Journal of Human Evolution 38, 2000, 497-521.

Gaudzinski et al. 1996: S. Gaudzinski / F. Bittmann / W. Boenigk / M. Frechen / T. Van Kolfschoten, Palaeoecology and Archaeology of the Kärlich-Seeufer Open-Air Site (Middle Pleistocene) in the Central Rhineland, Germany. Quaternary Research 46, 1996, 319-334.

2005: S. Gaudzinski / E. Turner / A. P. Anzidei / E. Alvarez-Fernandez / J. Arroyo-Cabrales / J. Cinq-Mars / V. T. Dobosi / A. Hannus / E. Johnson / S. C. Munzel / A. Scheer / P. Villa, The use of Proboscidean remains in everyday Palaeolithic life. Quaternary International 126-128, 2005, 179-194.

Gifford-Gonzalez 1999: D. Gifford-Gonzalez, Zooarchaeology in Africa: the first two million years. Archaeozoologia 10, 1999, 55-82.

Goren-Inbar / Lister / Werker / Chech 1994: N. Goren-Inbar / A. Lister / E. Werker / M. Chech, A Butchered elephant skull and associated artifacts from the Acheulian site of Gesher Benot Ya'Aqov, Israel. Paléorient 20, 1994, 99-112.

Graham / Beckerman / Thirgood 2005: K. Graham / A. P. Beckerman / S. Thirgood, Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. Biological Conservation 122, 2005, 159-171.

Grayson 1989: D. K. Grayson, Bone Transport, Bone Destruction, and Reverse Utility Curves. Journal of Archaeological Science 16, 1989, 643-652.

Hamilton / Bussne 1978: W. J. I. Hamilton / C. D. Bussne, Primate Carnivory and Its Significance to Human Diets. BioScience 28, 1978, 761-766.

Harding 1973: R. S. O. Harding, Predation by a troop of olive baboons (*Papio anubis*). American Journal of Physical Anthropology 38, 1973, 587-592.

1974: R. S. O. Harding, The predatory baboon. Expedition 16, 1974, 30-39.

Harding / Strum 1976: R. S. O. Harding / S. C. Strum, The predatory baboons of Kekopey. Natural History 85, 1976, 46-53.

Harmand et al. 2015: S. Harmand / J. E. Lewis / C. S. Feibel / C. J. Lepre / S. Prat / A. Lenoble / X. Boes / R. L. Quinn / M. Brenet / A. Arroyo / N. Taylor / S. Clement / G. Daver / J.-P. Brugal / L. Leakey / R. A. Mortlock / J. D. Wright / S. Lokorodi / C. Kirwa / D. V. Kent / H. Roche, 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521, 2015, 310-315.

Hausfater 1976: G. Hausfater, Predatory behavior of yellow baboons. Behaviour 56, 1976, 440-468.

Hayden 1981: B. Hayden, Subsistence and ecological adaptations of modern hunter / gatherers. In: R. S. O. Harding / G. Teleki (eds.), Omnivorous Primates: Gathering and Hunting in Human Evolution (New York 1981) 344-421.

Hemmer / Kahlke / Vekua 2011: H. Hemmer / R.-D. Kahlke / A. K. Vekua, The cheetah *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l. at the hominin site of Dmanisi (Georgia) – A potential prime meat supplier in Early Pleistocene ecosystems. Quaternary Science Reviews 30, 2011, 2703-2714.

Holliday/Steppan 2004: J. A. Holliday / S. J. Steppan, Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity. Paleobiology 30, 2004, 108-128.

Howell 1963: F. C. Howell, Noticia preliminar sobre el emplazamiento Acheulense de Torralba (Soria). Excavaciones arqueologicas en Espania 10, 1963, 1-38.

1966: F. C. Howell, Early Man. Time-Life International (The Netherlands 1966).

Howell et al. 1995: F. C. Howell / K. W. Butzer / L. G. Freeman / R. G. Klein, Observations on the Achelean occupation site of Ambrona (Soria province, Spain) with particular reference to recent investigations (1980-1983) and the lower occupation. Jahrbuch des Römisch-Germanischen Zentralmuseums 38 (Mainz 1995) 33-82.

Huguet Pamies et al. 2001: R. Huguet Pamies / C. Diez Fernandez-Lomana / J. Rosell Ardevol / I. Caceres Cuello de Oro / V. Moreno Lara / N. Ibanez Lopez / P. Saladié, Le gisement de Galería (Sierra de Atapuerca, Burgo, Espagne): un modèle archéozoologique de gestion du territoire au Pléistocène. L'Anthropologie 105, 2001, 237-257.

Huguet et al. 2013: R. Huguet / P. Saladié / I. Cáceres / C. Díez / J. Rosell / M. Bennàsar / R. Blasco / M. Esteban-Nadal / M. J. Gabucio / A. Rodríguez-Hidalgo / E. Carbonell, Successful subsistence strategies of the first humans in south-western Europe. Quaternary International 295, 2013, 168-182.

Isaac 1971: G. Isaac, The diet of early man: aspects of archaeological evidence from Lower and Middle Pleistocene sites in East Africa. World Archaeology 2, 1971, 279-298.

1978: G. Isaac, The food-sharing behavior of protohuman hominids. Scientific American 238, 1978, 90-108.

1984: G. Isaac, The archaeology of human origins: studies of the Lower Pleistocene in East Africa, 1971-1981. In: F. Wendorf / A. E. Close (eds.), Advances in World Archaeology Vol. 3 (Orlando 1984) 1-87.

Joordens et al. 2009: J. C. A. Joordens / F. P. Wesselingh / J. de Vos / H. B. Vonhof / D. Kroon, Relevance of aquatic environments for hominins: a case study from Trinil (Java, Indonesia). Journal of Human Evolution 57, 2009, 656-671.

Julien et al. 2015: M.-A. Julien / F. Rivals / J. Serangeli / H. Bocherens / N. J. Conard, A new approach for deciphering between single and multiple accumulation events using intra-tooth isotopic variations: Application to the Middle Pleistocene bone bed of Schöningen 13 II-4. Journal of Human Evolution 89, 2015, 114-128.

Kahlke/Gaudzinski 2005: R. D. Kahlke / S. Gaudzinski, The blessing of a great flood: Differentiation of mortality patterns in the large mammal record of the Lower Pleistocene fluvial site of Untermassfeld (Germany) and its relevance for the interpretation of faunal assemblages from archaeological sites. Journal of Archaeological Science 32, 2005, 1202-1222.

Kempf 2009: E. Kempf, Patterns of water use in primates. Folia Primatologica 80, 2009, 275-294.

Klein 1981: R. G. Klein, Stone Age predation on small African Bovids. South African Archaeological Bulletin 36, 1981, 55-65.

1982: R. G. Klein, Age (Mortality) Profiles as a Means of Distinguishing Hunted Species from Scavenged Ones in Stone Age Archaeological Sites. Paleobiology 8, 1982, 151-158.

1988: R. G. Klein, The archaeological significance of animal bones from Acheulean sites in southern Africa. The African Archaeological Review 6, 1988, 3-25.

Klein/Cruz-Uribe 1984: R. G. Klein / K. Cruz-Uribe, The Analysis of Animal Bones from Archeological Sites (Chicago-London 1984).

Klein/Allwarden/Wolf 1983: R. G. Klein / K. Allwarden / C. Wolf, The calculation and interpretation of ungulate age profiles from dental crown heights. In: G. Bailey (ed.), Hunter-Gatherer Economy in Prehistory: A European Perspective (Cambridge 1983) 47-57.

Klein et al. 2007: G. Klein / G. Avery / K. Cruz-Uribe / T. E. Steele, The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa. Journal of Human Evolution 52, 2007, 164-186.

Kreutzer 1992: L. A. Kreutzer, Bison and deer bone mineral densities: comparisons and implications for the interpretation of archaeological faunas. Journal of Archaeological Science 19, 1992, 271-294.

Kuitems et al. 2015: M. Kuitems / H. van der Plicht / D. G. Drucker / T. Van Kolfschoten / S. W. L. Palstra / H. Bocherens, Carbon and nitrogen stable isotopes of well-preserved, Middle Pleistocene bone collagen from Schöningen (Germany) and their palaeoecological implications. Journal of Human Evolution 89, 2015, 105-113.

Lam/Chen/Pearson 1999: Y. M. Lam / X. Chen / O. M. Pearson, Intertaxonomic Variability in Patterns of Bone Density and the Differential Representation of Bovid, Cervid, and Equid Elements in the Archaeological Record. American Antiquity 64, 1999, 343-362.

Leakey 1971: M. D. Leakey, Olduvai Gorge Vol. 3 (Cambridge 1971).

Lewis 1997: M. E. Lewis, Carnivoran paleoguilds of Africa: implications for hominid food procurement strategies. Journal of Human Evolution 32, 1997, 257-288.

Lewis/Werdelin 2010: M. E. Lewis / L. Werdelin, Carnivoran Dispersal Out of Africa During the Early Pleistocene: Relevance for Hominins? In: J. G. Fleagle / J. J. Shea / F. E. Grine / A. L. Baden / R. E. Leakey (eds.), Out of Africa I: The First Hominin Colonization of Eurasia, Vertebrate Paleobiology and Paleoanthropology (Dordrecht 2010) 13-26.

Lieberman et al. 2007: D. E. Lieberman / D. M. Bramble / D. A. Raichlen / J. J. Shea, The evolution of endurance running and the tyranny of ethnography: a reply to Pickering and Bunn (2007). Journal of Human Evolution 53, 2007, 439-442.

Lordkipanidze et al. 2007: D. Lordkipanidze / T. Jashashvili / A. Vekua / M. S. Ponce de León / C. P. E. Zollikofer / G. P. Rightmire / H. Pontzer / R. Ferring / O. Oms / M. Tappen / M. Bukhsianidze / J. Agustí / R. Kahlke / G. Kiladze / B. Martinez-Navarro / A. Mouskhelishvili / M. Nioradze / L. Rook, Postcranial evidence from early *Homo* from Dmanisi, Georgia. Nature 449, 2007, 305-310.

Lyman 1984: R. L. Lyman, Bone Density and Differential Survivorship of Fossil Classes. Journal of Anthropological Archaeology 3, 1984, 259-299.

1994: R. L. Lyman, Vertebrate Taphonomy (Cambridge 1994).

Marean 1989: C. W. Marean, Sabertooth cats and their relevance for early hominid diet and evolution. Journal of Human Evolution 18, 1989, 559-582.

Martínez et al. 2010: K. Martínez / J. Garcia / E. Carbonell / J. Agustí / J.-J. Bahain / H.-A. Blain / F. Burjachs / I. Cáceres / M. Duval / C. Falguères / M. Gómez / R. Huguet, A new Lower Pleistocene archeological site in Europe (Vallparadis, Barcelona, Spain). Proceedings of the National Academy of Sciences USA 107, 2010, 5762-5767.

Martinez-Navarro / Palmqvist 1996: B. Martinez-Navarro / P. Palmqvist, Presence of African Sabertoothed Felid *Megantereon whitei* (Broom, 1937) Mammalia, Carnivora, Machairodontinae in Apollonia-1 (Mygdonia Basin, Macedonia, Greece). Journal of Archaeological Science 23, 1996, 869-872.

McGrew 2001: W. McGrew, The other faunivory: Primate insectivory and early human diet. In: C. Stanford / H. Bunn (eds.), The Early Human Diet: The Role of Meat (Oxford 2001) 160-178.

McPherron et al. 2010: S. P. McPherron / Z. Alemseged / C. W. Marean / J. G. Wynn / D. Reed / D. Geraads / R. Bobe / H. A. Béarat, Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. Nature 466, 2010, 857-860.

Moigne / Barsky 1999: A.-M. Moigne / D. R. Barsky, Large mammal assemblages from Lower Palaeolithic sites in France: La Caune de L'Arago, Terra-Amata, Orgnac 3 and Cagny L'Épinette. In: S. Gaudzinski / E. Turner (eds.), The Role of Early Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages (Mainz 1999) 219-235.

Monahan 1996: C. M. Monahan, New zooarchaeological data from Bed II, Olduvai Gorge, Tanzania: implications for hominid behavior in the Early Pleistocene. Journal of Human Evolution 31, 1996, 93-128.

Moncel / Moigne / Combier 2005: M.-H. Moncel / A.-M. Moigne / J. Combier, Pre-Neandertal behaviour during isotopic stage 9 and the beginning of stage 8. New data concerning fauna and lithics in the different occupation levels of Orgnac 3 (Ardèche, South-East France): occupation types. Journal of Archaeological Science 32, 2005, 1283-1301.

Morris / Goodall 1977: K. Morris / J. Goodall, Competition for meat between chimpanzees and baboons of the Gombe National Park. Folia Primatologica 28, 1977, 109-121.

Musil 2007: R. Musil, Die Pferde von Schöningen: Skelettreste einer ganzen Wildpferdherde. In: H. Thieme (ed.), Die Schöninger Speere – Mensch und Jagd vor 400.000 Jahren (Stuttgart 2007) 136-140.

Niven et al. 2012: L. B. Niven / T. E. Steele / W. Rendu / J.-B. Mallye / S. P. McPherron / M. Soressi / J. Jaubert / J.-J. Hublin, Neandertal mobility and large-game hunting: the exploitation of reindeer during the Quina Mousterian at Chez-Pinaud Jonzac (Charente-Maritime, France). Journal of Human Evolution 63, 2012, 624-635.

O'Connell / Hawkes / Jones 1988: J. F. O'Connell / K. Hawkes / N. B. Jones, Hadza Scavenging: Implications for Plio/Pleistocene Hominid Subsistence. Current Anthropology 29, 1988, 356-363.

Palombo 2010: M. R. Palombo, A scenario of human dispersal in the northwestern Mediterranean throughout the Early to Middle Pleistocene. Quaternary International 223-224, 2010, 179-194.

Pante 2013: M. C. Pante, The larger mammal fossil assemblage from JK2, Bed III, Olduvai Gorge, Tanzania: implications for the feeding behavior of *Homo erectus*. Journal of Human Evolution 64, 2013, 68-82.

Pante et al. 2012: M. C. Pante / R. J. Blumenschine / S. D. Capaldo / R. S. Scott, Validation of bone surface modification models for inferring fossil hominin and carnivore feeding interactions, with reapplication to FLK 22, Olduvai Gorge, Tanzania. Journal of Human Evolution 63, 2012, 395-407.

Pickering / Bunn 2007: T. R. Pickering / H. T. Bunn, The endurance running hypothesis and hunting and scavenging in savanna-woodlands. Journal of Human Evolution 53, 2007, 434-438.

Pickering et al. 2004: T. R. Pickering / M. Domínguez-Rodrigo / C. P. Egeland / C. K. Brain, New data and ideas on the foraging behaviour of Early Stone Age hominids at Swartkrans Cave, South Africa. South African Journal of Science 100, 2004, 215-219.

2007: T. R. Pickering / M. Domínguez-Rodrigo / C. P. Egeland / C. K. Brain, Carcass foraging by early hominids at Swartkrans Cave (South Africa): a new investigation of the zooarchaeology and taphonomy of Member 3. In: T. R. Schick / N. Toth (eds.), Breathing Life into Fossils: Taphonomic Studies in Honor of C. K. (Bob) Brain (Gosport IN 2007) 233-253.

2008: T. R. Pickering / C. P. Egeland / M. Domínguez-Rodrigo / C. K. Brain / A. G. Schnell, Testing the "shift in the balance of power" hypothesis at Swartkrans, South Africa: Hominid cave use and subsistence behavior in the Early Pleistocene. Journal of Anthropological Archaeology 27, 2008, 30-45.

Piperno / Tagliacozzo 2001: M. Piperno / A. Tagliacozzo, The Elephant Butchery Area at the Middle Pleistocene site of Notarchirico (Venosa, Basilicata, Italy). In: G. Cavarretta / P. Gioia / M. Mussi / M. R. Palombo (eds.), Proceedings of the 1st International Congress the World of Elephants. CNR (Rome 2001) 220-226.

Pobiner 2007: B. L. Pobiner, Hominin-Carnivore Interactions: Evidence from Modern Carnivore Bone Modification and Early Pleistocene Archaeofaunas (Koobi Fora, Kenya; Olduvai Gorge, Tanzania) [Dissertation Rutgers University New Brunswick 2007].

Pobiner et al. 2008: B. L. Pobiner / M. J. Rogers / C. M. Monahan / J. W. K. Harris, New evidence for hominin carcass processing strategies at 1.5 Ma, Koobi Fora, Kenya. Journal of Human Evolution 55, 2008, 103-130.

Rabinovich / Biton 2011: R. Rabinovich / R. Biton, The Early-Middle Pleistocene faunal assemblages of Gesher Benot Ya'aqov: Inter-site variability. Journal of Human Evolution 60, 2011, 357-374.

Rabinovich / Gaudzinski-Windheuser / Goren-Inbar 2008: R. Rabinovich / S. Gaudzinski-Windheuser / N. Goren-Inbar, Systematic butchering of fallow deer (*Dama*) at the early middle Pleistocene Acheulian site of Gesher Benot Ya'aqov (Israel). Journal of Human Evolution 54, 2008, 134-149.

Rabinovich et al. 2012: R. Rabinovich / O. Ackermann / E. Aladjem / R. Barkai / R. Biton / I. Milevski / N. Solodenko / O. Marder, Elephants at the Middle Pleistocene Acheulian open-air site of Revadim Quarry, Israel. Quaternary International 276-277, 2012, 183-197.

Rendu et al. 2012: W. Rendu / S. Costamagno / L. Meignen / M.-C. Soulier, Monospecific faunal spectra in Mousterian contexts: Implications for social behavior. Quaternary International 247, 2012, 50-58.

Rivals/Kacimi/Moutoussamy 2004: F. Rivals / S. Kacimi / J. Moutoussamy, Artiodactyls, favourite game of prehistoric hunters at the Caune de l'Arago Cave (Tautavel, France). Opportunistic or selective hunting strategies? European Journal of Wildlife Research 50, 2004, 25-32.

Roberts/Parfitt 1999: M. B. Roberts / S. A. Parfitt, Boxgrove: A Middle Pleistocene Hominid Site at Earthen Quarry, Boxgrove, West Sussex (London 1999).

Rodríguez et al. 2011: J. Rodríguez / F. Burjachs / G. Cuenca-Bescós / N. García / J. van der Made / A. Pérez González / H.-A. Blain / I. Expósito / J. M. López-García / M. García Antón / E. Allué / I. Cáceres / R. Huguet / M. Mosquera / A. Ollé / J. Rosell / J. M. Parés / X. P. Rodríguez / C. Díez / J. Rofes / R. Sala / P. Saladié / J. Vallverdú / M. L. Bennasar / R. Blasco / J. M. Bermúdez de Castro / E. Carbonell, One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quaternary Science Reviews 30, 2011, 1396-1412.

2012: J. Rodríguez / G. Rodríguez-Gómez / J. A. Martín-González / I. Goikoetxea / A. Mateos, Predator–prey relationships and the role of Homo in Early Pleistocene food webs in Southern Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 365-366, 2012, 99-114.

Rodríguez-Hidalgo et al. 2015: A. Rodríguez-Hidalgo / P. Saladié / A. Ollé / E. Carbonell, Hominin subsistence and site function of TD10.1 bone bed level at Gran Dolina site (Atapuerca) during the late Acheulean. Journal of Quaternary Science 30, 2015, 679-701.

2016: A. Rodríguez-Hidalgo / F. Rivals / P. Saladié / E. Carbonell, Season of bison mortality in TD10.2 bone bed at Gran Dolina site (Atapuerca): Integrating tooth eruption, wear, and microwear methods. Journal of Archaeological Science: Reports 6, 2016, 780-789.

2017: A. Rodríguez-Hidalgo / P. Saladié / A. Ollé / J. L. Arsuaga / J. M. Bermúdez de Castro / E. Carbonell, Human predatory behavior and the social implications of communal hunting based on evidence from the TD10.2 bison bone bed at Gran Dolina (Atapuerca, Spain). Journal of Human Evolution 105, 2017, 89-122.

Rose 2001: L. Rose, Meat and the early human diet: Insights from Neotropical primate studies. In: C. Stanford / H. T. Bunn (eds.), The Early Human Diet: The Role of Meat (Oxford 2001) 141-159.

Russon et al. 2014: A. E. Russon / A. Compost / P. Kuncoro / A. Ferisa, Orangutan fish eating, primate aquatic fauna eating, and their implications for the origins of ancestral hominin fish eating. Journal of Human Evolution 77, 2014, 50-63.

Saccà 2012: D. Saccà, Taphonomy of *Palaeloxodon antiquus* at Castel di Guido (Rome, Italy): Proboscidean carcass exploitation in the Lower Palaeolithic. Quaternary International 276-277, 2012, 27-41.

Sahnouni et al. 2013: M. Sahnouni / J. Rosell / J. van der Made / J. M. Vergès / A. Ollé / N. Kandi / Z. Harichane / A. Derradji / M. Medig, The first evidence of cut marks and usewear traces from the Plio-Pleistocene locality of El-Kherba (Ain Hanech), Algeria: implications for early hominin subsistence activities circa 1.8 Ma. Journal of Human Evolution 64, 2013, 137-150.

Saladié et al. 2011: P. Saladié / R. Huguet / C. Díez / A. Rodríguez-Hidalgo / L. Cáceres / J. Vallverdú / J. Rosell / J. M. Bermúdez de Castro / E. Carbonell, Carcass transport decisions in *Homo antecessor* subsistence strategies. Journal of Human Evolution 61, 2011, 425-446.

Selvaggio 1994: M. M. Selvaggio, Carnivore tooth marks and stone tool butchery marks on scavenged bones: archaeological implications. Journal of Human Evolution 27, 1994, 215-228.

Selvaggio/Wilder 2001: M. M. Selvaggio / J. Wilder, Identifying the involvement of multiple carnivore taxa with archaeological bone assemblages. Journal of Archaeological Science 28, 2001, 465-470.

Semaw et al. 1997: S. Semaw / P. Renne / J. W. K. Harris / C. S. Feibel / R. L. Bernor / N. Fesseha / K. Mowbray, 2.5 million-year-old stone tools from Gona, Ethiopia. Nature 385, 1997, 333-336.

Serangeli et al. 2015: J. Serangeli / T. Van Kolfschoten / B. M. Starkovich / I. Verheijen, The European saber-toothed cat (*Homotherium latidens*) found in the "Spear Horizon" at Schöningen (Germany). Journal of Human Evolution 89, 2015, 172-180.

Shea/Sisk 2010: J. J. Shea / M. L. Sisk, Complex Projectile Technology and *Homo sapiens* Dispersal into Western Eurasia. PaleoAnthropology 2010, 100-122.

Shipman/Rose 1983: P. Shipman / J. Rose, Evidence of butchery and hominid activities at Torralba and Ambrona; an evaluation using microscopic techniques. Journal of Archaeological Science 10, 1983, 465-474.

Smith 2012: G. M. Smith, Hominin-Carnivore Interaction at the Lower Palaeolithic site of Boxgrove, UK. Journal of Taphonomy 10, 2012, 373-394.

2013: G. M. Smith, Taphonomic resolution and hominin subsistence behaviour in the Lower Palaeolithic: differing data scales and interpretive frameworks at Boxgrove and Swanscombe (UK). Journal of Archaeological Science 40, 2013, 3754-3767.

Speth 1989: J. D. Speth, Early hominid hunting and scavenging: the role of meat as an energy source. Journal of Human Evolution 18, 1989, 329-343.

Speth/Clark 2006: J. D. Speth / J. L. Clark, Hunting and overhunting in the Levantine Late Middle Palaeolithic. Before Farming 3, 2006, 1-42.

Speth/Tchernov 1998: J. D. Speth / E. Tchernov, The Role of Hunting and Scavenging in Neandertal Procurement Strategies: New Evidence from Kebara Cave (Israel). In: T. Akazawa (ed.), Neandertals and Modern Humans in Western Asia (New York 1998) 223-240.

2002: J. D. Speth / E. Tchernov, Middle Paleolithic tortoise use at Kebara Cave (Israel). Journal of Archaeological Science 29, 2002, 471-483.

Stanford 1995: C. B. Stanford, Chimpanzee hunting behavior. American Scientist 83, 1995, 256-261.

2001: C. B. Stanford, Hunting primates: A comparison of the predatory behavior of chimpanzees and human foragers. In: C. Stanford / H. T. Bunn (eds.), The Early Human Diet: The Role of Meat (Oxford 2001) 122-140.

Stanford et al. 1994: C. M. Stanford / J. Wallis / H. Matama / J. Goodall, Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, Tanzania, 1982-1991. American Journal of Physical Anthropology 94, 1994, 213-228.

Starkovich 2012a: B. M. Starkovich, Fallow Deer (*Dama dama*) Hunting During the Late Pleistocene at Klissoura Cave 1 (Peloponnese, Greece). Mitteilungen der Gesellschaft für Urgeschichte 21, 2012, 11-36.

2012b: B. M. Starkovich, Intensification of small game resources at Klissoura Cave 1 (Peloponnese, Greece) from the Middle Paleolithic to Mesolithic. Quaternary International 264, 2012, 17-31.

2014: B. M. Starkovich, Optimal Foraging, Dietary Change, and Site Use during the Paleolithic at Klissoura Cave 1 (Southern Greece). Journal of Archaeological Science 52, 2014, 39-55.

Starkovich / Conard 2015: B. M. Starkovich / N. J. Conard, Bone Taphonomy of the Schöningen "Spear Horizon South" and its Implications for Site Formation and Hominin Meat Provisioning. Journal of Human Evolution 89, 2015, 154-171.

Steele / Klein 2009: T. E. Steele / R. G. Klein, Late Pleistocene Subsistence Strategies and Resource Intensification in Africa. In: J.-J. Hublin / M. P. Richards (eds.), The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence (Dordrecht 2009) 113-126.

2005: T. E. Steele / R. G. Klein, Mollusk and tortoise size as proxies for stone age population density in South Africa: Implications for the evolution of human cultural capacity. Munibe (Anthropologia-Arkeologia) 57, 2005, 221-237.

Steele / Weaver 2002: T. E. Steele / T. D. Weaver, The Modified Triangular Graph: A Refined Method for Comparing Mortality Profiles in Archaeological Samples. Journal of Archaeological Science 29, 2002, 317-322.

Stewart et al. 2008: A. M. E. Stewart / C. H. Gordon / S. A. Wich / P. Schroor / E. Meijaard, Fishing in *Macaca fascicularis:* A rarely observed innovative behavior. International Journal of Primatology 29, 2008, 543-548.

Stewart 1994: K. M. Stewart, Early hominid utilisation of fish resources and implications for seasonality and behaviour. Journal of Human Evolution 27, 1994, 229-245.

2010: K. M. Stewart, The case for exploitation of wetlands environments and foods by pre-sapiens hominins. In: S. C. Cunnane / K. M. Stewart (eds.), Human Brain Evolution (New Jersey 2010) 137-171.

Stiner 1990: M. C. Stiner, The Use of Mortality Patterns in Archaeological Studies of Hominid Predatory Adaptations. Journal of Anthropological Archaeology 9, 1990, 305-351.

1994: M. C. Stiner, Honor Among Thieves: a Zooarchaeological Study of Neandertal Ecology (Princeton 1994).

2002: M. C. Stiner, Carnivory, coevolution and the geographic spread of genus *Homo*. Journal of Archaeological Research 10, 2002, 1-63.

2005: M. C. Stiner, The Faunas of Hayonim Cave, Israel: a 200,000-Year Record of Paleolithic Diet, Demography and Society. American School of Prehistoric Research Bulletin 48. Peabody Museum of Archaeology and Ethnology, Harvard University (Cambridge 2005).

Stiner 2009: M. C. Stiner, Prey choice, site occupation intensity & economic diversity in the Middle – early Upper Palaeolithic at the Üçağızlı Caves, Turkey. Before Farming 3, 2009, 1-20.

Stiner / Barkai / Gopher 2009: M. C. Stiner / R. Barkai / A. Gopher, Cooperative hunting and meat sharing 400-200 kya at Qesem Cave, Israel. Proceedings of the National Academy of Sciences USA 106, 2009, 13207-132012.

Stiner / Barkai / Gopher 2011: M. C. Stiner / R. Barkai / A. Gopher, Hearth-side socioeconomics, hunting and paleoecology during the late Lower Paleolithic at Qesem Cave, Israel. Journal of Human Evolution 60, 2011, 213-233.

Stiner / Munro / Surovell 2000: M. C. Stiner / N. D. Munro / T. A. Surovell, The Tortoise and the Hare: Small-Game Use, the Broad-Spectrum Revolution, and Paleolithic Demography. Current Anthropology 41, 2000, 39-73.

Stopp 1993: M. P. Stopp, Taphonomic analysis of the faunal assemblage. In: R. Singer / B. G. Gladfelter / J. J. Wymer (eds.), The Lower Palaeolithic Site at Hoxne, England (Chicago, London 1993) 138-149.

Strum 1981: S. C. Strum, Processes and products of change: Baboon predatory behavior at Gilgil, Kenya. In: R. S. O. Harding / G. Teleki (eds.), Omnivorous Primates: Gathering and Hunting in Human Evolution (New York 1981) 255-302.

Surbeck / Hohmann 2008: M. Surbeck / G. Hohmann, Primate hunting by bonobos at LuiKotale, Salonga National Park. Current Biology 18, 2008, 906-907.

Thieme 1997: H. Thieme, Lower Palaeolithic hunting spears from Germany. Nature 385, 1997, 807-810.

2000: H. Thieme, Lower Palaeolithic Hunting Weapons from Schöningen, Germany: The Oldest Spears in the World. Acta Anthropologica Sinica 19, 2000, 140-147.

2005: H. Thieme, The Lower Paleolithic art of hunting: the case of Schöningen 13 II-4, Lower Saxony, Germany. In: C. Gamble / M. Porr (eds.), The Hominid Individual in Context: Archaeological Investigations of Lower and Middle Paleolithic Landscapes, Locales and Artifacts (London, New York 2005) 115-132.

2007: H. Thieme, Überlegungen zum Gesamtbefund des Wildpferd-Jagdlagers. In: H. Thieme (ed.), Die Schöninger Speere – Mensch und Jagd vor 400.000 Jahren (Stuttgart 2007) 177-190.

Thompson et al. 2015: J. C. Thompson / S. P. McPherron / R. Bobe / D. Reed / W. A. Barr / J. G. Wynn / C. W. Marean / D. Geraads / Z. Alemseged, Taphonomy of fossils from the hominin-bearing deposits at Dikika, Ethiopia. Journal of Human Evolution 86, 2015, 112-135.

Turner 1988: A. Turner, Relative Scavenging Opportunities for East and South African Plio-Pleistocene Hominids. Journal of Archaeological Science 15, 1988, 327-341.

1992: A. Turner, Large carnivores and earliest European hominids: changing determinants of resource availability during the Lower and Middle Pleistocene. Journal of Human Evolution 22, 1992, 109-126.

Ungar / Grine / Teaford 2006: P. S. Ungar / F. E. Grine / M. F. Teaford, Diet in Early *Homo*: A Review of the Evidence and a New Model of Adaptive Versatility. Annual Review of Anthropology 35, 2006, 209-228.

Van Kolfschoten 2014: T. Van Kolfschoten, The Palaeolithic locality Schöningen (Germany): A review of the mammalian record. Quaternary International 326-327, 2014, 469-480.

Van Kolfschoten / Buhrs / Verheijen 2015: T. Van Kolfschoten / E. Buhrs / I. Verheijen, The larger mammal fauna from the Lower Palaeolithic Schöningen Spear site and its contribution to hominin's subsistence. Journal of Human Evolution 89, 2015, 138-153.

Villa et al. 2005: P. Villa / E. Soto / M. Santonja / A. Pérez-González / R. Mora / J. Parcerisas / C. Sesé, New data from Ambrona: closing the hunting versus scavenging debate. Quaternary International 126-128, 2005, 223-250.

Voormolen 2008: B. Voormolen, Ancient Hunters, Modern Butchers: Schöningen 13II-4, a kill-butchery site dating from the northwest European Lower Paleolithic [Dissertation Leiden University 2008].

Waechter 1968: J. Waechter, Swanscombe 1968. Proceedings of the Royal Anthropological Institute of Great Britain and Ireland for 1968, 53-61.

1969: J. Waechter, Swanscombe 1969. Proceedings of the Royal Anthropological Institute of Great Britain and Ireland for 1969, 83-95.

1976: J. Waechter, Man Before History (London 1976).

Watts/Mitani 2002: D. P. Watts / J. C. Mitani, Hunting behavior of adolescent male chimpanzees at Ngogo, Kibale National Park, Uganda. American Journal of Physical Anthropology 23, 2002, 1-28.

Weaver/Boyko/Steele 2011: T. D. Weaver / R. H. Boyko / T. E. Steele, Cross-platform program for likelihood-based statistical comparisons of mortality profiles on a triangular graph. Journal of Archaeological Science 38, 2011, 2420-2423.

Wenban-Smith 2013: F. Wenban-Smith, Discussion and conclusions: Clactonian elephant hunters, north-west European colonisation and the Acheulian invasion of Britain? In: F. Wenban-Smith (ed.), The Ebbsfleet Elephant: Excavations at Southfleet Road, Swanscombe in Advance of High Speed 1, 2003-2004 (Oxford 2013) 447-474.

Werdelin/Lewis 2005: L. Werdelin / M. E. Lewis, Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns. Zoological Journal of the Linnean Society 144, 2005, 121-144.

2013: L. Werdelin / M. E. Lewis, Temporal change in functional richness and evenness in the eastern African plio-pleistocene carnivoran guild. PLOS ONE 8, 2013, e57944.

Wrangham 1977: R. Wrangham, Feeding behavior of chimpanzees in Gombe National Park, Tanzania. In: T. H. Clutton-Brock (ed.), Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys, and Apes (New York 1977) 504-538.

Yravedra 2010: J. Yravedra / M. Domínguez-Rodrigo / M. Santonja / A. Pérez-González / J. Panera / S. Rubio-Jara / E. Baquedano, Cut marks on the Middle Pleistocene elephant carcass of Áridos 2 (Madrid, Spain). Journal of Archaeological Science 37, 2010, 2469-2476.

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