‘We hunt to share’: social dynamics and very large mammal butchery during the Oldowan–Acheulean transition

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ABSTRACT
The Early Pleistocene (2.58–0.78 Ma) was a period of major evolutionary changes in the hominin lineage. The progressive consolidation of bipedal locomotion, alongside increases in cranial capacity and behavioural flexibility, allowed early Homo to exploit an increasing diversity of resources and environmental settings within the changing landscapes of East Africa and beyond. These complex processes were not necessarily linear or spatially uniform, given the technological diversity documented, particularly during the Oldowan–Acheulean transition. In this paper, we argue that human populations experienced a considerable demographic expansion from c.1.7–1.5 Ma onwards, expressed in the number, size, density, and distribution of archaeological sites. These patterns resulted from the interplay of high-yielding animal resource exploitation strategies, technological investment, prosocial behaviours as well as increasingly structured land use patterns. A more consolidated hominin demographic structure led to the extinction of large sympatric carnivore species, while larger group sizes would have led to more successful Out-of-Africa dispersals.

1. Introduction: the role of demography and social networks in multi-causal explanations of human evolutionary processes

The Pleistocene (2.58–0.01 Ma) was a long period of major evolutionary changes in the hominin lineage. For over 2 million years, an emergent and recurrent set of unifacial and/or bifacial technological sequences ascribed to either the Oldowan or the Acheulean (and sometimes featuring in both technocomplexes) were at the core of hominin behavioural strategies. Initial assessments were under the impression that these continuities in the lithic record were indicative of considerable behavioural stasis in the Early and Middle Pleistocene, derived from presumed cognitive constraints (cf. Isaac 1972; Leakey 1975; Binford 1989; Mithen 1996). However, there has been an increasing recognition that assemblages spanning the Oldowan–Acheulean transition were considerably more morphologically and techno-functionally diverse at local and supra-regional scales than was previously acknowledged. Alternative explanations now place more emphasis on demographic variables, such as the size, stability, and interconnectedness of past human populations (Nowell and White 2010; Kuhn 2012; French 2016), as well as their learning transmission methods (Lycett and
Gowlett 2008; Shipton 2010; Rossano 2017). Nowell and White (2010) argue that the small scale and limited degree of interconnectivity and foraging range of thinly spread hominin populations made the transmission and maintenance of innovations unlikely, hindering cumulative cultural dynamics (Shennan 2009; Premo and Kuhn 2010; Premo 2012; Hopkinson, Nowell, and White 2013; Collard et al. 2016). It is also possible that the effective technological solutions granted by platform preparation strategies for flake production and Large Cutting Tools (LCTs) may have led to a preference for adaptive conservatism in the technological realm (Finkel and Barkai 2018), with perishable material culture perhaps experiencing different innovation rates than their lithic counterparts (Hurcombe 2014).

Palaeolithic demography is a notoriously elusive archaeological signature (Pike-Tay 2000; French 2016), yet it is a fundamental dimension for understanding human evolutionary processes and behavioural innovations. Even if the long-term reproductive strategies of surviving populations will resemble optimal fitness-maximizing models (Shennan 2009), population trends are often driven by short-term individual prospects based on prior social experiences (French 2016) and the extent of landscape knowledge (Clark and Linares-Matás 2020; Linares-Matás and Lim 2021). A crucial demographic dimension that emerges from this multi-scalar tension and is often neglected in discussions of Early Pleistocene societies is the fact that metapopulation stasis with near-zero growth rates is uncharacteristic of any natural fertility population observed (Winterhalder et al. 1988; Bentley, Jasienska, and Goldberg 1993; Hill and Hurtado 1996). Therefore, these trends are most likely the outcome of long-term averaging periods of endogenously generated demographic fluctuations; such fluctuations would have involved exponential increases with subsequent regulation through mortality spikes or population dispersals (Boone 2002). Reproductive success tends to involve strategies of offspring resource and energy allocation that are flexibly adapted to environmental constraints and opportunities (e.g. Hill 1993; O’Connell, Hawkes, and Blurton Jones 1999; Winterhalder and Smith 2000; Read and LeBlanc 2003; Bird and O’Connell 2006; Shennan 2008). As such, these boom-bust population dynamics, also observed in the population ecology of many other animal species (Ostfeld and Keesing 2000), have the potential to increase population fitness and diversity beyond the predictions derived from stable equilibrium models (Doebeli, Jaque, and Ispolatov 2021); these implications are of great interest in the study of early human evolution.

In modern hunter-gatherer societies, social living reduces the daily variance in food acquisition, mitigating an important source of risk (Winterhalder 1986; Janssen and Hill 2014). At the same time, high exclusion costs, alongside social obligations of resource redistribution, tend to result in little correlation between the amount of large-game resources that individual foragers acquire and the amount they or their immediate families consume (Speth 1983; Smith 1985; Hawkes 1993; Speth 2010; Bird et al. 2013). In this context, reputation and trust are important drivers of indirect reciprocity and altruistic behaviours relying on assortative interaction at the population level (Eshel and Cavalli-Sforza 1982; Nowak and Sigmund 2005; Ohtsuki et al. 2006; Henrich and Henrich 2007). These processes imply that selection pressures influencing individual association, transmission of resources or information, and band formation are most likely taking place simultaneously at the individual and the (meta) group level (van Baalen and Rand 1998; Apicella et al. 2012).

As such, we argue in this paper that high-yielding food-acquisition strategies involving large and very large animals (Table 1) are more likely to emerge in the context of (meta) group-level provisioning, since this scenario would allow hunters and their families to reap the benefits associated with the elevated net nutritional returns of animal tissue consumption (Domínguez-Rodrigo et al. 2014), while simultaneously enhancing the social standing of the providers (Hawkes 1991; Hawkes, O’Connell, and Coxworth 2010) through prosocial behaviours that compensate for
Table 1. Classification of African fauna on the basis of size class and weight ratios, following Bunn (1982). Average weight and estimated meat (and fat) yields can vary significantly, on the basis of sex, age, season, etc, although it generally represents around 60% of the carcass weight. In our text, ‘large’ refers to size 4, and ‘very large’ refers to sizes 5 and 6.

| Size Class | Weight ratio | Example | Average Weight | Estimated meat yield | Reference |
|------------|--------------|---------|----------------|----------------------|-----------|
| 1          | <50 kg       | Springbok, Antidorcas marsupialis, Impala, Aepyceros melampus | 32 kg           | 25.6 kg              | Galofré and Fábregas (1983) |
| 2          | 50–125 kg    | Grant’s gazelle, Gazella granti | 60 kg           | 37.8 kg              | Hoffman et al. (2020) |
| 3a         | 125–250 kg   | Gemsbok, Oryx gazella, Blue wildebeest, Connochaetes taurinus | 187 kg          | 96 kg                | Van Heerden (2018) |
| 3b         | 250–500 kg   | Burchell’s zebra, Equus quagga burchellii | 321 kg          | 193.2 kg             | Hoffman, Geldenhuys, and Cawthorn (2016) |
| 4          | >500–1,000 kg | Common eland, Taurotragus oryx | 798 kg          | 480 kg               | Galofré and Fábregas (1983) |
| 5          | 1,000–4,000 kg | Hippopotamus amphibius, White rhinoceros, Ceratotherium simum | 1,400 kg | 800 kg | |
| 6          | >4,000 kg    | African bush elephant, Loxodonta africana | 3,800 kg | 2,000 kg | Davis and Reeves (1990) |

variations in carcass acquisition rates (Gurven and Hill 2009; Speth 2010; Tomasello et al. 2012; Bird et al. 2013). In this paper, we review the African archaeological record before and after the Oldowan–Acheulean transition, with a particular emphasis on BK (Olduvai) and other East African localities exhibiting exploitation of large and very large animal carcasses, in relation to emergent social and ecological factors associated with a greater reliance on megafauna, including carnivore palaeoguild dynamics.

2. The East African Early Pleistocene record

East Africa has been the focus of intense archaeological and palaeoanthropological research for nearly a hundred years, with the aim of unravelling the patterns of environmental change and the evolutionary processes of early hominins, including aspects of their biological adaptations, subsistence strategies, technological behaviour, and social organisation. The Early Pleistocene climatic trends towards increasing cooling show punctuated increases in variability, seasonality, and aridity, factors that lead to increasingly open mosaic habitats in East Africa (Bobe and Behrensmeyer 2004; deMenocal 2004; Cerling et al. 2011; Blumenfeld et al. 2019).

In terms of anatomy, the Early Pleistocene African record shows that the early Homo lineage experienced an expansion of the brain and the body, sexual dimorphism decreased, cheek teeth became reduced in size, and limb proportions and cranial morphology became more similar to those of later hominins (Walker and Leakey 1993; McHenry and Coffing 2000; Antón and Snodgrass 2012; Antón, Potts, and Aiello 2014). Bony labyrinth structure is a crucial adaptation in the unconscious perception of movement and the evolution of bipedal locomotion, with Homo erectus being the earliest hominin species with an anatomically modern morphology (Spoor, Wood, and Zonneveld 1994). Elongation of the lower limbs was another particularly important adaptation in the context of obligate bipedalism (Ruff and Walker 1993), since relative walking travel costs in
**Homo erectus** are nearly half those estimated for the skeletal architecture of *Australopithecus afarensis* (Steadel-Numbers and Tilkens 2004; Steudel-Numbers 2006; Pontzer, Raichlen, and Sockol 2009). The Ilor footprints (Kenya, 1.5 Ma) provide direct evidence of a longitudinally arched foot with energy-saving medial weight transfer of pressure in *H. erectus* (Hatala et al. 2016). The fibula is another important skeletal element involved in bipedal locomotion, since it plays an important role in transmitting hindlimb loads; the tibial strength ratios documented for *Homo erectus* further confirm that this species was fully adapted to terrestrial bipedality (Marchi et al. 2019). Moreover, the degree of developmental (or phenotypic) plasticity exhibited by *H. erectus* is also linked to the ability to disperse successfully beyond the environmental range of previous hominins (Antón et al. 2016).

The emergence of the Acheulean, with a focus on bifacial tools, has been documented around 1.76–1.74 Ma at the sites of Kokiselei 4 (West Turkana, Kenya) and Konso (Ethiopia), and around 1.7–1.66 Ma at FLK-West (Olduvai Gorge, Tanzania), in the East African Rift (Lepre et al. 2011; Beyene et al. 2013; Diez-Martín et al. 2015). This innovative method, which stems from the technological repertoire previously exhibited by Oldowan hominins, enabled the generation of a greater amount of sharp edge per unit of raw material. It was also deployed to make bifacial large cutting tools (LCTs), which effectively combine strength and shape through long and durable cutting edges able to undertake a wide range of tasks (Kleindienst 1961; Leakey 1971; Diez-Martín and Eren 2012; de la Torre 2016; Gallotti and Mussi 2018). Important dimensions in this process were familiarity with the properties and distribution of high-quality raw material sources, and control of knapping sequences through core preparation and volume management (Semaw, Rogers, and Stout 2009; Shipton 2010; Gallotti 2013; Diez-Martín et al. 2014a; Sánchez-Yustos et al. 2017). The versatility and manual portability of prepared cores, reflected in the spatio-temporal fragmentation of operational sequences, synergises nicely with the obligate terrestrial bipedalism of *Homo erectus* – the species with which this technocomplex is generally associated. The combination of these traits, alongside more developed landscape knowledge networks, would have helped enable a more structured exploitation of increasingly open environments with patchy resource distributions, as documented for example at the Peninj complex, near the shores of Lake Natron, Tanzania (de la Torre, Mora, and Martínez-Moreno 2008; Domínguez-Rodrigo, Alcalá, and Luque 2009a; Diez-Martín et al. 2014a; Clark and Linares-Matás 2020). Between 1.6 and 1.4 Ma, Acheulean technologies are found throughout the African continent (Sahnouni, Semaw, and Rogers 2013b) and soon afterwards also into Eurasia (Bar-Yosef and Goren-Inbar 1993).

With regard to subsistence, and while small- and medium-sized carcasses remain relevant, the Oldowan–Acheulean transition is characterized by a progressive increase in the proportion and frequency of large and very large animal carcasses exploited by early hominins (Surovell, Waguespack, and Brantingham 2005), often at water-margin habitats (Domínguez-Rodrigo et al. 2014; Table 2). At FwJj20, Koobi Fora Formation, Kenya (1.95 Ma) there are cut-marks on the ventral side of a rhinoceros rib and on a hippopotamus astragalus (Braun et al. 2010). More abundant evidence for hippopotamus and large mammal butchery comes from other Koobi Fora localities, such as Gaji 0/ and GaJi 5, in deposits dating to 1.5 Ma (Bunn 1994). Cut-marks on hippopotamus limb bones and a rib have similarly been documented at the Algerian site of El Kherba (1.8 Ma), one of them overlain by a carnivore tooth mark, which evidences hominin primary access (Sahnouni et al. 2013a). Butchery activities around 1.3 Ma have also been identified on garrifflid remains at the site of PEES4 at Peninj, Tanzania (Domínguez-Rodrigo et al. 2009a) and on the limb bones of large bovids, hippopotami and crocodiles at Buia, Eritrea (Delfino et al. 2004; Fiore et al. 2004). At Bouri (1 Ma, Ethiopia), butchery of large bovids and hippopotamus has also been documented (Asfaw et al. 2002).
**Table 2.** African Early Pleistocene and early Middle Pleistocene archaeological localities with megafaunal remains. Most of these open-air sites have direct evidence of hominin exploitation of very large carcasses.

| Site                          | Chronology                     | Lithic technology | Taphonomic evidence | Megafaunal species       | References                                                                 |
|-------------------------------|--------------------------------|-------------------|---------------------|--------------------------|-----------------------------------------------------------------------------|
| Kanjera (Kenya)               | Lower Pleistocene, 2 Ma.       | Oldowan           | Association         | Hippopotamus             | Ferraro et al. (2013)                                                      |
| Fejej FI-1 (Ethiopia)          | Lower Pleistocene, > 1.9 Ma    | Oldowan           | Association         | Elephant (Teeth)         | Asfaw et al. (1991)                                                        |
| El Kherda, Ain Hanech (Algeria)| Lower Pleistocene 1.8 Ma       | Oldowan           | CM                  | Hippopotamus             | Sahnouini et al. (2013a)                                                   |
| FLKN 6 (Olduvai, Tanzania)    | Lower Pleistocene bed I        | Oldowan           | CM                  | Elephant                 | Domínguez-Rodrigo, Barba, and Egeland (2007) and Leakey (1971)             |
| HWK-EE (Olduvai, Tanzania)    | Lower Pleistocene 1.7–1.5 Ma   | Developed Oldowan | CM-astragalus       | Elephant                 | Yravedra et al. (2017a)                                                   |
| FLKW (Olduvai, Tanzania)      | Lower Pleistocene Bed II, 1.69 Ma | Acheulean      | Association         | Elephant, Hippopotamus   | Leakey, 1971                                                              |
| FLKN bed II (Olduvai, Tanzania)| Lower Pleistocene 1.7–1.2 Ma | Developed Oldowan | Association         | Elephant                 | Semav et al 2020                                                           |
| Gona Dan 5 (Ethiopia)         | Lower Pleistocene 1.6 Ma       | Acheulean         | CM                  | Elephant                 | Berthelet and Chavaillon (1996), Berthelet and Chavaillon (2001), Berthelet (2001) |
| Barogali (Djibouti)           | Lower Pleistocene 1.6–1.3 Ma.  | Oldowan           | CM                  | Elephant and Hippopotamus|                                                |
| Koobi Fora (Kenya), several localities | Lower Pleistocene 1.5 Ma. | Developed Oldowan | CM                  | Hippopotamus             | Bunn (1994) and Pobiner et al. (2008)                                      |
| SHK (Olduvai, Tanzania)       | Lower Pleistocene 1.5 Ma       | Developed Oldowan | CM                  | Hippopotamus             | Domínguez-Rodrigo et al. (2014)                                           |
| TK (Olduvai, Tanzania)        | Lower Pleistocene 1.5 Ma.      | Acheulean         | Association         | Sivatherion, Elephas, Hippopotamus | Yravedra et al. (2016), Rubio Jara et al. (2017) and Panera et al. (2019) |
| ST (Peninj, Tanzania)         | Lower Pleistocene 1.4 Ma.      | Acheulean         | CM                  | Giraffid                 | Domínguez-Rodrigo et al. (2002)                                           |
| BK 3.1 (Olduvai, Tanzania)    | Lower Pleistocene 1.3 Ma.      | Developed Oldowan | CM                  | Hippopotamus             | Yravedra et al. (2019a)                                                   |
| BK 4b (Olduvai, Tanzania)     | Lower Pleistocene 1.3 Ma.      | Developed Oldowan | CM                  | Elephant                 | Domínguez-Rodrigo et al (2014)                                            |
| BK 4 c (Olduvai, Tanzania)    | Lower Pleistocene 1.3 Ma.      | Developed Oldowan | CM                  | Elephant                 | Organista et al. (2017)                                                   |
| BK 5 (Olduvai, Tanzania)      | Lower Pleistocene 1.3 Ma.      | Developed Oldowan | CM                  | Elephant                 | Organista et al (2016)                                                     |
| JK (Olduvai, Tanzania)        | Lower-Middle Pleistocene bed III, 1 Ma. | Acheulean      | CM                  | Hippopotamus             | Yravedra et al. (2020)                                                    |
| Daka Member Bouri (Ethiopia)  | Lower Pleistocene 1 Ma.        | Acheulean         | CM                  | Hippopotamus             | Asfaw et al (2002)                                                        |

(Continued)
| Site                        | Chronology                  | Lithic technology | Taphonomic evidence       | Megafaunal species | References                                      |
|-----------------------------|-----------------------------|-------------------|---------------------------|--------------------|------------------------------------------------|
| Buia (Ethiopia)             | Lower Pleistocene 1 Ma.      | Developed Oldowan | CM femur, tibiae calcaneus | Hippopotamus       | Fiore et al (2004)                              |
| Olorgesailie 15, (Kenya)    | Lower Pleistocene 0.97 Ma.   | Acheulean         | CM (rib)                  | Elephant           | Potts, Behensmeyer, and Ditchfield (1999)       |
| PDK (Olduvai, Tanzania)     | Lower-Middle Pleistocene bed IV | Acheulean         | CM                        | Elephant           | Leakey (1994)                                   |
| WK (Olduvai, Tanzania)      | Lower-Middle Pleistocene bed IV | Acheulean         | CM                        | Elephant and Hippopotamus | Leakey (1994)                                   |
| Heb (Olduvai, Tanzania)     | Lower-Middle Pleistocene bed IV | Acheulean         | CM                        | Elephant           | Leakey (1994)                                   |
| Hargufia A-2 (Middle Awash, Ethiopia) | Early Middle Pleistocene | Acheulean         | CM                        | Hippopotamus       | Clark et al. (1984)                             |
| Gombore II (Mek Kunture, Ethiopia) | Early Middle Pleistocene | Acheulean         | CM                        | Hippopotamus       | Altamura, Mussi, and Melis (2017, 2018)         |
| Ndung’a (Nachukui Formation, Kenya) | Early Middle Pleistocene | Acheulean         | CM                        | Elephant (Single carcass) | Delagnes et al. (2006)                         |
In Olduvai, the earliest evidence of megafaunal exploitation comes from FLK North (Bed I, 1.8 Ma) in the form of a single giraffid metapodial with cut-marks (Domínguez-Rodrigo et al. 2010). A giraffid tibia shaft and hippopotamid remains, including a mandible, have also been reported as evidencing large mammal butchery at HWK-EE, dated to 1.7 Ma (Pante et al. 2018). In Bed II, hominin occupations expanded beyond lake-side environments, into more varied ecological settings, including inland fluvial contexts (Hay 1976). Level 5 of FLK-West (1.7 Ma, Lower Bed II) has cut-marks on a large bovid (size 4) tibia and a metatarsal (Yravedra et al. 2017a), and at SHK (1.5 Ma), there are two hippopotamus ribs with cut-marks and one limb bone with percussion marks (Domínguez-Rodrigo et al. 2014b). However, the site with the clearest and most consistent evidence of megafaunal exploitation in Olduvai, and indeed Early Pleistocene East Africa, is BK (Bell’s Korongo), which also witnessed the first large-scale excavation conducted by the Leakey team in Olduvai (Leakey 1954, 1965).

3. BK: recurrent megafaunal exploitation in the Early Pleistocene of East Africa

BK is an Upper Bed II open-air site located just above Tuff IID (1.35 Ma), on the southern side of the Side Gorge, 3 km upstream from the Main Gorge junction (Olduvai, Tanzania). It consists of a series of low-energy alluvial and fluvial decantation deposits corresponding to a medial to distal fan zone and a floodplain facies (Leakey 1971; Uribelarrea del Val and Domínguez-Rodrigo 2017). During the formation of upper Bed II, BK was located by a small stream, south of seasonal ponds (Hay 1976). Most of the assemblage was deposited on the stream bank, with preserved material subsequently washed into the immediate channel fill, given the good degree of bone preservation and the high frequencies of lithic debitage (Leakey 1971; Monahan 1996; Egeland and Domínguez-Rodrigo 2008; Diez-Martín et al. 2009). While the extent to which hominins played a primary role in the accumulation of most Bed II faunal assemblages is unclear, several lines of evidence indicate that BK is primarily anthropogenic in origin, although some inputs from carnivore activity and other natural processes were also incorporated into the sequence (Egeland and Domínguez-Rodrigo 2008). On palaeoecological grounds, the taxonomic diversity and density of remains is greater than documented on natural background scatters (Bunn 1982; Behrensmeyer 1983; Potts 1988; Blumenschine 1989; Sept 1994; Tappen 1995; Egeland and Domínguez-Rodrigo 2008). The taxonomic profile of faunal remains suggests a very productive open ecosystem with riverine woodlands and permanent water sources, consistent with the geomorphological reconstruction of the site and its immediate environment, as described above. Pieces of ostrich eggshell are unusually plentiful at BK (Leakey 1971), and Stewart (1994) has reported the presence of very large catfish (Clarias sp.) specimens at BK exhibiting traces of anthropogenic processing, likely associated with very late dry or early wet season deposition.

Recent excavations by the TOPPP team have exposed a surface of 45 m² at the site, showing how most archaeological levels at BK have archaeological materials preferentially concentrated within 15/20 cm horizons with lower densities in between (Domínguez-Rodrigo et al. 2009b; Domínguez-Rodrigo et al. 2014; Yravedra et al. 2019a). Inferences from bone taphonomy show systematic and recurrent hominin butchery of large and very large mammals (including Pelorovis, Syncerus, Sivatherium, Hippopotamus, and Elephas), with abundant defleshing and evisceration cut-marks, a very high number of percussion marks, and low levels of carnivore damage in most levels throughout the sedimentary sequence (Table 3; Domínguez-Rodrigo et al. 2009b; Domínguez-Rodrigo et al. 2014; Organista et al. 2016; Yravedra et al. 2019a). Even proboscidean remains show a pattern of intensive breakage by hominins
Table 3. Summary of taphonomic data for the different levels of BK (Olduvai Gorge).

| Level | NISP Small | NISP Medium | NISP Large/Very Large | Lithics | CM on Large | PM on Large | TM on Large | References |
|-------|------------|-------------|-----------------------|---------|-------------|-------------|-------------|------------|
| BK1   | 36         | Unreported  | 119                   | 216     | 14 (11.7%)  | 27 (22.6%)  | 7 (5.9%)    | Domínguez-Rodrigo et al. (2009b) and |
| BK2   | 66         | Unreported  | 245                   | 321     | 37 (15.1%)  | 41 (16.8%)  | 14 (5.7%)   | Diez-Martín et al. (2009)            |
| BK3   | 27         | 127         | 68                    | 614     | 9 (13.2%)   | 8 (11.7%)   | 0 (0.0%)    |                                      |
| BK4   | 79         | 379         | 412                   | 424     | 16 (3.9%)   | 22 (5.34%)  | 8 (1.9%)    | MDR et al. (2014) and                |
| BK5   | 33         | 76          | 125                   | 59      | 12 (9.6%)   | 9 (7.2%)    | 8 (6.4%)    | Organista et al. (2016)             |
| BK U3.1 | 6         | 41          | 13                    | 17      | 3 (23.07%)  | 2 (15.38%)  | 0 (0.0%)    | Yravedra et al. (2019a)            |

(Domínguez-Rodrigo et al. 2014). Monahan (1996) and Egeland (2007) already noted anthropogenic evidence on the Leakey faunal remains, but had to treat them as a single assemblage due to limited stratigraphic control. The abundance of taphonomic evidence for anthropogenic exploitation, coupled with the absence of axial and lower-utility elements resilient to density-mediated attrition processes (e.g. metapodials), suggest that hominins transported and processed high-utility skeletal portions of small and medium-sized carcasses (Monahan 1996; Faith and Gordon 2007; Egeland and Domínguez-Rodrigo 2008; Organista et al. 2016).

The even skeletal representation and the high frequency of skulls belonging to larger carcasses would be more consistent with on-the-spot processing of substantially fleshy carcasses, with some of these likely representing natural deaths (Domínguez-Rodrigo et al. 2014; Organista et al. 2016). Cut-mark frequencies and the percussion/carnivore ratios are more consistent with hammerstone-to-carnivore early access scenarios (Blumenschine 1988; Capaldo 1998; Gidna, Kisui, and Domínguez-Rodrigo 2014). As such, hyaena alterations at the site likely derive from secondary access to hominin refuse in the context of intermittent site use, given the considerable number of individual episodes of carcass processing registered in the BK sequence (Bunn 2006; Egeland and Domínguez-Rodrigo 2008). The concentration of water, vegetation, and other resources along the channel banks was favoured by numerous animals, including hominins, although it is worth noting that similar river channel contexts within the Bed II Olduvai palaeolandscape (e.g. PLK, WK, HK) have not yielded comparable bone accumulations (Uribelarrea del Val and Domínguez-Rodrigo 2017; Yravedra et al. 2019a).

In terms of the lithic assemblage, stone knapping sequences at BK targeted the production of relatively small flakes, mostly on quartz/quartzite, alongside several bifacial shaped tools (Leakey 1971; de La Torre and Mora 2005; Diez-Martín et al. 2009; Sánchez-Yustos et al. 2016). The preferential selection of quartz over basalt in flake manufacture has a functional explanation, since quartz flakes are more efficient in butchery tasks than basalt flakes (Schick and Toth 1993; Sánchez-Yustos et al. 2016). The advent of computational approaches to the study of bone surface modifications, such as cut-marks, is proving successful in the identification of implement type and lithic raw materials employed in butchery activities (Courtenay et al. 2019b; Linares-Matás et al. 2019; López-Cisneros et al. 2019; Maté-González et al. 2019; Yravedra et al. 2019b). At BK in particular, flakes made from high-quality quartzites with a fine granular composition were being preferentially selected for these tasks (Yravedra et al. 2017b; Courtenay et al. 2019a).

Manuports and hammerstones with clear battering signs and detached surface scars were likely involved in freehand and bipolar knapping (Diez-Martín et al. 2009), and some unmodified ones may have been used in bone percussion activities or for other activities, such as nut-cracking, plant processing, or for tenderizing meat (cf. de La Torre et al. 2013; Sánchez-Yustos et al. 2015; 2016;
Arroyo et al., 2016; Linares-Matás and Clark 2021). Relatively complex reduction sequences are documented throughout the BK sequence, frequently involving core rotation and elongation on multifacial/multipolar cores and bifacial multipolar centripetal hierarchized cores, among others, and resulted in the intensive exploitation and maximisation of raw material, often to the point of core exhaustion (Diez-Martín et al. 2009; Sánchez-Yustos et al. 2017; Yravedra et al. 2019a).

Retouched flakes in the BK assemblage (c.5%), mostly on quartz (>88%; Sánchez-Yustos et al. 2017), may have been oriented towards heavier-duty tasks, given that they are reported as ‘slightly larger, thicker and heavier than plain flakes’ (Diez-Martín et al. 2009). Recent experimental studies have shown that flake retouch and larger flake sizes increase force loading and manipulability, thus enhancing wood processing efficiency (Bencomo Viala et al. 2020; Gürbüz and Lycett 2021). It is likely that hominins at BK and elsewhere at this time fashioned organic tools, such as digging sticks and/or hunting implements. The presence of some handaxes and other bifacial LCTs documented at BK4b also seems to point in this direction (Sánchez-Yustos et al. 2016). Interestingly, in the assemblage studied by Diez-Martín et al. (2009), only 4% of flakes belong to initial reduction stages, and 73% of flakes do not exhibit cortical areas, and Sánchez-Yustos et al. (2017) document similar core preparation strategies at SHK and BK. This pattern implies that hominins were bringing prepared cores with them in anticipation of a need for flakes in the context of increasingly predictable and profitable very large carcass acquisition strategies.

4. Discussion
There is increasing evidence for the co-evolutionary nature of genetic phenotypical expression and cultural practices in the human lineage, particularly in the context of high-fidelity learning environments and strong selective pressures (e.g. Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Laland, Odling-Smee, and Feldman 2000). As such, understanding the causal pathways in the emergence of prosociality is necessarily a multi-disciplinary endeavour.

4.1. Seasonality and megafaunal exploitation
The potential influence of seasonal fluctuations in hominin behaviour has long been recognized, but it is still an incipient, albeit increasingly relevant, area of research (Speth and Davis 1976; Speth 1987; Bunn and Ezzo 1993; Foley 1993; Pante et al. 2018; Rivals et al. 2018; Domínguez-Rodrigo et al. 2019; Linares-Matás and Clark 2021). Palaeoclimatic records emphasise the importance of seasonal fluctuations of increasing amplitude throughout the Early Pleistocene in East Africa (Blumenthal et al. 2019). In open mosaic environments, these trends would have resulted in periods of low above-ground water and plant biomass availability, with physiological consequences for ungulates, which likely experienced periods of fat-depletion on a recurring basis (Sinclair 1975; Linares-Matás and Clark 2021). This scenario entails important selective pressures in terms of hominin behaviour: Cordain et al. (2000) argue that in the context of ungulate fat depletion, hunter-gatherers would either preferentially target fatter individuals and carcass portions, increase their consumption of carbohydrate-rich plant resources, or hunt larger animals with greater proportions of body fat. As noted by Linares-Matás and Clark (2021), Oldowan hominins were already deploying the first two strategies by 2.195 Ma through the targeting of ungulate brains and viscerae at Kanjera South, Kenya (Ferraro et al. 2013), as well as by incorporating freshwater resources to their diet at FwJ20, Kenya (Braun et al. 2010; Archer et al. 2014). It is very plausible that later Homo erectus also engaged
in similar seasonal behavioural adaptations, particularly once they incorporated food processing, including tendering and cooking – given evidence of hominin engagement with fire plausibly beginning around this time (Gowlett et al. 1981; Berna et al. 2012). Food processing practices would have considerably enhanced the digestibility and net nutritional returns of dietary resources, particularly meat and tubers (Wrangham et al. 1999).

Furthermore, opportunistic consumption of larger terrestrial and aquatic taxa at localities such as Gona OGS-6, FwJj20, HWK EE, or Buia (Fiore et al. 2004; Braun et al. 2010; Cáceres et al. 2017; Pante et al. 2018) may have emerged in contexts of seasonal stress towards the end of the dry season and early in the wet season (Linares-Matás and Clark 2021), in line with the third predicted alternative outlined by Cordain et al. (2000). These periods would have also provided easier access opportunities to megafaunal carcasses, since resource limitation also appears to be one of the main causes of mortality among very large taxa in the Serengeti (Sinclair, Mduma, and Brashares 2003). Similarly, these seasonal transitions also provide the best opportunities for procurement of large catfish without specialized technology, and there is evidence of anthropogenic exploitation of these fish taxa at both BK and FwJj20 (Stewart 1994; Archer et al. 2014). While some sedimentary units at BK represent time-averaged assemblages (Organista et al. 2016), tooth wear data suggest that BK 5, with evidence for megafaunal exploitation, entailed single-season occupations (Domínguez-Rodrigo et al. 2019). At BK U3.1, geoarchaeological evidence show that the level formed over less than a year, with sedimentation occurring during the wet season (Yravedra et al. 2019a), which implies that hominin activities took place during the preceding dry season and/or in the early wet season, prior to the quick and low energy flooding event that covered the assemblage.

### 4.2. Demographic dynamics and subsistence strategies

The mode of procurement of very large carcasses, either by scavenging or by hunting, is very difficult to infer from taphonomic or zooarchaeological data (Delagnes et al. 2006). It is very likely that the recurrent exploitation of natural deaths provided opportunities for megafaunal consumption, and it is true that very large animals, such as hippopotami and elephants, possess very thick skins, complicating hunting activities for carnivores and hominins alike. Nonetheless, more active procurement strategies may also be necessary to explain this novel hominin dietary niche, involving the systematic exploitation of large and very large animals, particularly during the second half of the Early Pleistocene onwards.

The more efficient locomotion documented for Homo erectus in relation to previous hominin taxa (cf. Steudel-Numbers 2006; Pontzer, Raichlen, and Sockol 2009) would have reduced mobility costs, a limiting factor in hunter-gatherer group sizes, and facilitated greater population densities, since larger groups, particularly those exploiting terrestrial animal resources, require greater mobility to meet collective dietary requirements (Binford 2001; Kelly 2003; Grove 2009; French 2016). Furthermore, since prey size correlates with frequency of food-sharing in modern hunter-gatherer societies (Kaplan et al. 1985), the energy-dense spaces of megafaunal carcass acquisition and processing would have acted as particularly attractive locales of enhanced sociality and nucleation. Groups of at least 16 individuals are recorded in the footprint trails at Ileret (1.5 Ma), in the context of consolidated bipedal locomotion adaptations (Hatala et al. 2016). Seasonal aggregations of larger group sizes, typical of multi-level modular primate societies in open-air and arid environments (e.g. Grüter and Zinner 2004; Grueter, Chapais, and Zinner 2012; Swedell and Plummer 2012), would have constituted an important anti-predator defence mechanism among hominins lacking specialised climbing
abilities, particularly when they approached contested spaces, such as permanent freshwater sources (Isbell et al. 2018; Chazan 2021). Larger and well-coordinated group sizes would have also facilitated the procurement of very large animals through the targeting of less predatory individuals by approaching within close striking distance (e.g. Surovell, Waguespack, and Brantingham 2005), since social carnivores experience a positive correlation between pack size and prey size, net energetic returns, and pursuit success (Kruuk 1972; Creel and Creel 1995; Carbone et al. 1999). Nonetheless, since we may envision considerable temporal variance in large and very large animal acquisition rates, the survival of larger groups and foraging units would have (also) depended on the seasonal and inter-annual outcomes of more reliable and predictable foraging strategies incorporating geophytes, berries, and likely other resources, such as invertebrates, honey, small game, etc. (Hawkes, Hill, and O’Connell 1982; Hawkes 1993; Kaplan et al. 2000; Lupo and Schmitt 2002; Bliege Bird and Bird 2008; Bliege Bird, Codding, and Bird 2009; Linares-Matás and Clarke 2021).

Strategies enabling a more consistent intake of high-quality dietary products would in turn have favoured selection of behavioural and cognitive traits that facilitated reciprocity, cooperation, and other social interactions (Foley and Lee 1991; Aiello and Dunbar 1993; Aiello and Wheeler 1995; Milton 1999; Wrangham et al. 1999; Bunn 2001; Foley 2001; Kudo and Dunbar 2001; Shultz, Nelson, and Dunbar 2012; Gowlett et al. 2015; Stade and Gamble 2019; Goren-Inbar and Belfer-Cohen 2020). Furthermore, the kin-bonding potential of these social mechanisms would allow the consolidation of cooperative child-rearing and the evolution of empathy, likely through the simultaneous influence of parental provisioning and alloparenting strategies including the assistance of post-reproductive females (Hawkes, O’Connell, and Blurton Jones 1997; O’Connell, Hawkes, and Blurton Jones 1999; Hrdy 2009; Antón and Snodgrass 2012; Spikins 2012). The offset of reproductive costs, alongside reductions in mortality risks associated with social anti-predator strategies, would have been a powerful driver of demographic growth in Homo erectus societies in East Africa, particularly during the second half of the Early Pleistocene.

We argue that this demographic expansion is clearly reflected in the marked increase in the number, size, density, and distribution of archaeological sites in East Africa (Figure 1 and Tables 4 and 5). A similar increase in the number and density of sites, as well as in terms of interassemblage variability, has also been documented in southern Africa over the course of the Acheulean (Deacon 1975; Figure 1).

### 4.3. Hominin carnivory and palaeoecological dynamics

The demographic increase and the dietary niche expansion of early Homo in East Africa ought to be examined also in relation to long-term dynamics of the carnivore palaeoguild throughout the Early Pleistocene, since a greater reliance on animal resources would have entailed a coevolutionary process that generated reciprocal selective pressures associated with overlapping dietary and habitat ranges among sympatric species (Turner 1990; Brantingham 1998; Werdelin and Lewis 2005, 2013; Faurby et al. 2020). The large carnivore guild incorporates species with body mass equal or greater than 21.5 kg, a threshold value in carnivore ecology, since these species generally capture prey of their own body mass or greater (Carbone et al. 1999). Early hominins started to consistently acquire meat from mammalian carcasses from the start of the Early Pleistocene (e.g. Bunn 1982; Dominguez-Rodrigo et al. 2005; Dominguez-Rodrigo, Barba, and Egeland 2007; Braun et al. 2010; Ferraro et al. 2013; Parkinson et al. 2018). This behaviour would have resulted in some degree of character displacement (i.e. behavioural divergence) and niche partitioning among the
Figure 1. Distribution map of African early pleistocene localities: (a) before and (b) after 1.7 Ma. Courtesy of Jonathan Lim.
**Table 4.** African Early Pleistocene sites older than 1.7 Ma, used to generate distribution and heat maps.

| Site                          | Technocomplex | Chronology | Key References                                      |
|-------------------------------|---------------|------------|-----------------------------------------------------|
| Gona (Ethiopia) several localities | Oldowan       | 2.6–2.4 Ma | Semaw et al. (1997)                                  |
| Bouri (Ethiopia)              | Oldowan       | 2.5 Ma     | de Heinzelin et al. (2000)                          |
| Hadar (Ethiopia) Several localities | Oldowan     | 2.6–2.52 Ma | Hovers (2001)                                        |
| Omo 57 (Ethiopia)             | Oldowan       | 2.36–2.34 Ma | Chavaillon (1976), Howell, Haesaerts, and de Heinzelin (1987) and Merrick (1976) |
| Omo 84 (Ethiopia)             | Oldowan       |            |                                                     |
| Omo 71 (Ethiopia)             | Oldowan       |            |                                                     |
| Omo 123 (Ethiopia)            | Oldowan       |            |                                                     |
| Omo 204 FtJ1 (Ethiopia)       | Oldowan       |            |                                                     |
| Omo 396 FtJ2 (Ethiopia)       | Oldowan       |            |                                                     |
| Kanjera (Kenya)               | Oldowan       | 2 Ma       | Plummer et al. (1999)                                |
| Fejej (Ethiopia)              | Oldowan       | 1.9 Ma     | Asfaw et al. (1991)                                 |
| W. Turkana (Kenya)            | Oldowan       | 2.3 Ma     | Roche et al. (1999)                                 |
| Lokalalei LA2C (Kenya)        | Oldowan       | 2.24 Ma    | Roche et al. (1999) and Brown                       |
| Lokalalei LA 1 (Gajh 5) (Kenya)| Oldowan     | 2.33 Ma    | and Gathogo (2002)                                  |
| Nachukui (Kenya)              | Oldowan       | 2.3 Ma     | Roche et al. (2003)                                 |
| Senga 5 (Congo)               | Oldowan       | 2 Ma       | Harris et al. (1987)                                |
| Chiwondo (Malawi)             | Oldowan       | 2 Ma       | Kafulu and Stern (1987)                             |
| Koobi Fora (Kenya)            | Oldowan       | 1.9 Ma     | Isaac, Harris, and Crader (1976, 1997)              |
| Ain Hanech (Algeria)          | Oldowan       | 1.8 Ma     | Sahnouni (1998) and Sahnouni et al. (2002)          |
| DK Olduvai (Tanzania)         | Oldowan       | 1.9 Ma     | Leakey (1971)                                       |
| MK Olduvai (Tanzania)         | Oldowan       | 1.9 Ma     |                                                     |
| FLK NN Olduvai (Tanzania)     | Oldowan       | 1.8 Ma     |                                                     |
| FLK-Zinj Olduvai (Tanzania)   | Oldowan       | 1.76 Ma    |                                                     |
| HWK EE, Olduvai (Tanzania)    | Oldowan       | ~1.7 Ma    | Pante and de La Torre (2018)                        |
| Sterkfontein (South Africa)   | Oldowan       | 2–1.5 Ma   | Kuman (1998)                                        |
| Tardiguet-er-Raha (Morocco)   | Oldowan       | >2 Ma      | Biberson (1961)                                     |
| Douar Doum (Morocco)          | Oldowan       | >2 Ma      |                                                     |
| Sidi Abderrahman (Morocco)    | Oldowan       | 2–1.8 Ma   |                                                     |
| Kokiselei 5 (Kenya)           | Acheulean     | 1.8 Ma     | Chevrier (2012) and Lepre et al. (2011)             |
| Kokiselei 4 (Kenya)           | Acheulean     | 1.76 Ma    |                                                     |
| Konso-Gardula 6 KGA6-A1 (Ethiopia) | Acheulean | 1.75 Ma    | Beyene et al. (2013)                                |
| Melka Kunture (Ethiopia)      | Oldowan       | 1.7 Ma     | Chavaillon and Piperno (1975) and Chavaillon et al. (1979) |

**Table 5.** African Early Pleistocene sites younger than 1.7 Ma, used to generate the distribution and heat maps.

| Site                          | Technocomplex | Chronology | References                                           |
|-------------------------------|---------------|------------|------------------------------------------------------|
| Bouri (Ethiopia) de Heinzelin et al. (1999) | Acheulean | 1–0.5 Ma | de Heinzelin et al. (2000) and Schick and Toth (2017) |
| Gadeb (Ethiopia) Gadeb 2 (2C, 2B, 2E) | Acheulean | 1.45–0.7 Ma | Clark and Kurashina (1979a, 1979b) and de La Torre (2011) |
| Konso-Gardula KGA4-A2 (Ethiopia) | Acheulean | ~1.6 Ma | Asfaw et al. (1992)                                  |
| Konso-Gardula KGA10-A11 (Ethiopia) | Acheulean | ~1.45 Ma |                                                     |
| Konso-Gardula KGA10-A6 (Ethiopia) | Acheulean | ~1.44–1.43 Ma |                                                     |
| Konso-Gardula KGA7-A1, A3 (Ethiopia) | Acheulean | ~1.4 Ma |                                                     |
| Konso-Gardula KGA7-A2/ KGAB-A1 (Ethiopia) | Acheulean | ~1.4–1.3 Ma |                                                     |
| Konso-Gardula KGA12-A1 (Ethiopia) | Acheulean | ~1.25 Ma |                                                     |
| Dawaitoli Formation, Awash Ethiopia | Acheulean | 1.0 Ma | Schick and Clark (2003)                              |

(Continued)
| Site                                      | Technocomplex | Chronology       | References                                                                 |
|------------------------------------------|---------------|------------------|---------------------------------------------------------------------------|
| BSN-17 Gona (Ethiopia)                   | Acheulean     | ~1.7–1.5 Ma      | Semaw et al. (2018) and Semaw et al. (2020)                                |
| DAN-5 Gona (Ethiopia)                    | Acheulean     | ~1.6–1.5 Ma      |                                                                           |
| OGS-12 Gona (Ethiopia)                   | Acheulean     | ~1.6–1.5 Ma      |                                                                           |
| OGS-5 Gona (Ethiopia)                    | Acheulean     | ~1.6 Ma          |                                                                           |
| BSN-12 Gona (Ethiopia)                   | Acheulean     | ~1.2 Ma          |                                                                           |
| Melka Wakena (Ethiopia) MW5              | Acheulean     | 1.62–1.34 Ma     | Hovers et al. (2021)                                                      |
| Melka Wakena (Ethiopia) MW2              | Acheulean     | 1.62–1.34 Ma     |                                                                           |
| Melka Kunture (Ethiopia) Garba IVD        | Acheulean     | 1.7–1.4 Ma       | Gallotti et al. (2010), Gallotti et al. (2014) and Gallotti and Mussi (2017) |
| Atebella II (Melka Kunture-Ethiopia)     | Acheulean     | 1.0 Ma           |                                                                           |
| Simbrio III (Melka Kunture-Ethiopia)     | Acheulean     | 1.0 Ma           |                                                                           |
| Cornelia (Melka Kunture-Ethiopia)        | Acheulean     | 1 Ma             | Brink et al. (2012)                                                      |
| Gambore II y III, (M. Kunture Ethiopia)  | Acheulean     | 1.7–1.4 Ma       | Gallotti et al. (2010), Gallotti et al. (2014), and Gallotti and Mussi (2017, 2021) |
| Garba I (Melka Kunture, Ethiopia)        | Acheulean     | 1.0 Ma           |                                                                           |
| Garba IIIC (Melka Kunture, Ethiopia)     | Acheulean     |                  |                                                                           |
| Garba XII (Melka Kunture, Ethiopia)      | Acheulean     |                  |                                                                           |
| Garba XIII (Melka Kunture, Ethiopia)     | Acheulean     |                  |                                                                           |
| Koobi Fora (Kenya) FxJj21                | Acheulean     | ~1.41 Ma         | Isaac, Harris, and Crader (1976) and Isaac, Harris, and Kroll (1997)      |
| Koobi Fora (Kenya) FxJj37                | Acheulean     |                  |                                                                           |
| Koobi Fora (Kenya) FxJj63                | Acheulean     |                  |                                                                           |
| Koobi Fora (Kenya) FxJj65                | Acheulean     |                  |                                                                           |
| Chesowanja (Kenya) GnJi 1/6E             | Acheulean     | ~1.4 Ma          | Gallotti et al. (1981) and Harris and Gowlett (1980)                      |
| Olorgesailie member 1 (Kenya)            | Acheulean     | 0.99–0.97 Ma     | Isaac (1977) and Potts, Behrensmeier, and Ditchfield (1999)               |
| Isinya, (Kenya)                          | Acheulean     | 0.974 Ma         | Roche et al. 1988, Durkee and Brown (2014)                                |
| Kariandusi, (Kenya)                      | Acheulean     | 0.97 Ma          | Shipton (2011)                                                            |
| Karari, (Kenya)                          | Acheulean     | 1.6–1.2 Ma       | Harris (1978)                                                             |
| EF-HR Olduvai (Tanzania)                 | Acheulean     | 1.66–1.33 Ma     | Leakey (1971) and de La Torre and Mora (2018)                            |
| FC West Olduvai (Tanzania)               | Acheulean     | >1.3 Ma          | Leakey (1971)                                                             |
| CK Olduvai (Tanzania)                    | Acheulean     | >1.35 Ma         |                                                                           |
| Elephant I Olduvai (Tanzania)            | Acheulean     | >1.35 Ma         |                                                                           |
| SHK Olduvai (Tanzania)                   | Acheulean     | 1.5 Ma           | Leakey (1971) and Diez-Martín et al. (2014b)                              |
| TK Olduvai (Tanzania)                    | Acheulean     | >1.35 Ma         | Leakey (1971), Panera et al. (2019) and Rubio Jara et al. (2017)          |
| BK Olduvai (Tanzania)                    | Acheulean     | <1.35 Ma         | Leakey (1971)                                                             |
| MNK Principal Olduvai (Tanzania)         | Acheulean     | ~1.3 Ma          | Leakey (1971)                                                             |
| JK Olduvai (Tanzania)                    | Acheulean     | 1.0 Ma           | Pante (2013)                                                              |
| FLK-West Olduvai (Tanzania)              | Acheulean     | 1.69             | Diez-Martin et al. (2015) and Yravedra et al (2017)                       |
| Peninj (Tanzania)                        | Acheulean     | 1.6–1.2          | de La Torre, Mora, and Martinez-Moreno (2008)                             |
| Peninj (Tanzania) ES2-Lepolosi           | Acheulean     | 1.6–1.4          |                                                                           |
| Rietputs 15 (South Africa)               | Acheulean     | < 1.6            | Kuman and Gibbon (2018)                                                   |
| Sterkfontein (South Africa)              | Acheulean     | 1.6–1.4          |                                                                           |
| Swartkrans (South Africa)                | Acheulean     | 1.6–1.4          |                                                                           |
| Vaal Rivers (South Africa)               | Acheulean     | < 1.5            |                                                                           |
| Wonderwerk (South Africa)                | Acheulean     | >1.07 Ma         | Berna et al. 2012 and Shaar et al. (2021)                                 |
| Elandsfontein (South Africa)             | Acheulean     | 1 Ma             | Klein et al. (2007), Braun et al. (2013) and Presnyakova (2019)           |
| Nyabusosi NY18 (Uganda)                  | Developed Oldowan | 1.5 Ma        | Texier (1995)                                                             |
| Thomas Quarry 1 Casablanca (Morocco)     | Acheulean     | 0.989 ± 0.208    | Rhodes et al. (2006) and Geraads, Raynal, and Eisenmann (2004)            |
| Barogali (Djibouti)                      | Developed Oldowan | 1.6–1.3       | Berthelet (2002)                                                          |

(Continued)
Table 5. (Continued).

| Site                        | Techno-complex       | Chronology          | References                                      |
|-----------------------------|----------------------|---------------------|------------------------------------------------|
| Ain Boucherit (Algeria)     | Developed Oldowan    | 1                   | Sahnouni, Van Der Made, and Everett (2011)     |
| Palmerinhas (Angola)        | Developed Oldowan    | 1.5                 | Clark (1991)                                   |
| Mwaganda’s Village (Malawi) |                      | Early Middle       | Clark (1990)                                   |
|                             |                      | Pleistocene         |                                                |

carnivore guild (Brown and Wilson 1956; Brantingham 1998). However, since there is a systemspecific limit to the amount of tolerable resource utilization overlap, increasing pressure associated with a greater degree of niche encroaching – in this case through hunting and perhaps some degree of confrontational scavenging – would eventually reach a critical point potentially leading to competitive exclusion (MacArthur and Levins 1967; Tillman 1982; Brantingham 1998; Faurby et al. 2020).

The East African carnivore guild has been shown to have lost progressively most of its functional richness throughout the Late Pliocene and the Early Pleistocene, in a protracted process over hundreds of thousands of years, but dropping dramatically around 2–1.5 Ma, with turnover and extinction rates peaking from 1.8 Ma onwards (Werdelin and Lewis 2013; Faurby et al. 2020). Hypercarnivores and long-faced social canids were most affected closer to 1.5 Ma (Werdelin and Lewis 2013). While macroevolutionary processes show how carnivore diversity is tightly linked to climate-determined fluctuations in herbivore biomass and diversity (Sandom et al. 2013; Fritz et al. 2016), environmental factors, such as variations in temperature or precipitation, appear unrelated to the trends observed in East Africa, and those palaeocological factors that do exhibit an important degree of correlation, such as changes in tree cover, did not impact functional richness or species diversity in other non-anthropogenic ecosystems, such as North America (Werdelin and Lewis 2013; Faurby et al. 2020). The decline of East African carnivore palaeoguilds may therefore be explained by the progressive introduction of early Homo into the carnivore niche space throughout the Early Pleistocene (Walker and Shipman 1989; Brantingham 1998; Werdelin and Lewis 2005, 2013; Faurby et al. 2020).

While the targeting of prime-aged individuals has been proposed as a hallmark of the hominin predatory niche (e.g. Stiner 2013), the process of niche encroaching during the Oldowan at FLK-Zinj and Kanjera South appears to have entailed primarily a systematic targeting of seasonally vulnerable bovid demographics (Bunn and Pickering 2010; Ferraro et al. 2013; Oliver et al. 2019; Linares-Matás and Clark 2021), followed by hominins actively expanding their predatory niche by engaging in megafaunal consumption later in the Early Pleistocene (e.g. Bunn 1994; Monahan 1996; Fiore et al. 2004; Sahnouni et al. 2013a; Domínguez-Rodrigo et al. 2014b; Yravedra et al. 2019a). These macroevolutionary changes affecting the carnivore palaeoguild of East Africa are reflected in the zooarchaeological and palaeoecological record of Olduvai: felid signatures, prominent in Bed I assemblages, gave way to stronger hyaenid signatures at most Bed II assemblages (Egeland and Domínguez-Rodrigo 2008), a pattern consistent with diachronic changes in trophic dynamics in which active hominin carcass procurement strategies became increasingly prominent at the expense of the hypercarnivore niche. Since omnivores tend to live in much greater densities than specialised carnivores (Walker and Shipman 1989; Pedersen, Faurby, and Svenning 2017), the combined meat intake of a growing hominin population, with increasingly larger brains and sophisticated behavioural adaptations, led to the competitive exclusion of many large carnivore taxa (Faurby et al. 2020). A similar phenomenon of hominin encroachment on
hypercarnivore niches is also emerging in the late Early Pleistocene record of southern Europe (e.g. Palombo et al. 2008; García Garriga, Martínez, and Yravedra 2017; Madurell-Malapeira et al. 2017; Linares-Matás et al. 2021; Yravedra et al. 2021). Stiner (2013) further suggests that an emphasis on prime-aged individuals of large animal species from the late Middle Pleistocene onwards may have represented an additional ‘galvanisation’ of the hominin predatory niche, although she also notes the considerable variability documented on actualistic and prehistoric human-generated mortality profiles.

5. Conclusions

A sophisticated cognitive apparatus, a diverse and high-quality diet incorporating large and very large animals, efficient bipedal locomotion, advanced landscape planning, and prosocial interactions allowed early Homo communities in East Africa to form and maintain larger group sizes than earlier hominins, at least seasonally (Figure 2). The active procurement and butchery of very large prey, documented with increasing frequency through the Early Pleistocene, would have created ample opportunities for food sharing, a key factor for understanding the social dynamics of the Oldowan–Acheulean transition. The offset of
reproductive costs through food provisioning, alongside reductions in mortality risks associated with social anti-predator strategies and reductions in carnivore competition, appear to have promoted demographic growth among African *Homo erectus* societies, as reflected in the marked increase in the number, size, density, and distribution of archaeological sites during the second half of the Early Pleistocene. A more consolidated demographic structure involving larger group sizes may have also favoured even more successful Out-of-Africa dispersals during the late Early and early Middle Pleistocene, since dispersals would have also functioning as a mechanism to regulate the sustainability of regional hominin population ecologies. The development and application of analytical approaches aiming to characterize the nature and seasonality of carcass acquisition strategies in the context of hominin exploitation of very large animals would contribute to further advance these palaeoanthropological debates.

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