The Role of Landscape Knowledge Networks in the Early Pleistocene Technological Variability of East Africa

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Abstract

Early human behaviour was related to the social knowledge of the landscape through an awareness of the spatio-temporal distribution of resources and the ability to successfully exploit that resource network. In this paper, we explore the dynamics of raw material procurement, technological manufacture and tool use in several Early Pleistocene assemblages from the Oldowan and Early Acheulean of East Africa. We argue that investment in lithic assemblages would have been dependent on the accumulation and consolidation of environmental knowledge through the adoption of food-procurement strategies allowing for predictable access to highly-ranked resources in open and seasonal environments. Integrating the plasticity of social knowledge networks as a population-dependent process with the relationship between procurement strategies and resource predictability within the landscape provides an interpretive framework that can explain and illustrate the broad scale technological differences present in Early Pleistocene assemblages.

Introduction

The Early Pleistocene (~2.58–0.77 Ma) encompasses the 'Oldowan' and 'Acheulean' Early Stone Age traditions[1], with the former defined by the production of sharp stone flakes mostly detached from a core by direct percussion with rare secondary modification (Gallotti 2018) and the latter defined by large, elongated, symmetrical and bifacially-flaked artefacts (Shea 2013, 2020). Core-and-flake technologies precede Acheulean technologies in Africa (e.g. Braun et al. 2008, 2009, 2019; Gallotti and Mussi 2015; Hovers et al. 2002; Leakey 1971; Roche et al. 1999; Semaw et al. 1997, 2003), West Asia (e.g.

[1] The first stone tools may be found as far back as 3.3 Ma in the Pliocene at Lomekwi-3 (Harmand et al. 2015; but see Domínguez-Rodrigo and Alcalá 2019). These are excluded from discussion here due to their isolated occurrence and their chronological position falling outside the temporal scope of this paper.

Tchernov 1999) and Europe (e.g. Arzarello et al. 2007, 2012; Carbonell et al. 1999; Parés et al. 2006; Toro-Moyano et al. 2011). In Europe, this pattern occurs despite the earliest occupation(s) occurring after Acheulean appearance in the Levant (Bar-Yosef and Goren-Inbar 1993; Goren-Inbar et al. 2000).

In Africa, the Oldowan appears around the Plio-Pleistocene boundary (2.6–2.5 Ma) at the Ethiopiean sites of Ledi-Geraru and Gona (Braun et al. 2019; Semaw et al. 2003; Stout et al. 2010), while the Acheulean appears 1.8–1.6 Ma at Kokiselei-4 (Kenya), Konso Gardula (Ethiopia) and FLK-West (Tanzania) (Beyene et al. 2013; Diez-Martín et al. 2015; Lepre et al. 2011). The temporal persistence of both traditions has led some authors to argue for long periods of relative internal technological stasis and a relatively large (cognitive) change between them (e.g. Corbey et al. 2016; Semaw et al. 2009; Wynn 2002). Neuroimaging studies show more diverse neural activation during late Acheulean handaxe production than for Oldowan reduction (Stout et al. 2008, 2011). Nonetheless, we suggest that these studies cannot be straightforwardly applied to the Oldowan-Acheulean boundary since late Acheulean handaxes require a distinct cognitive imposition of form and a volumetric treatment of reduction which have not been consistently demonstrated in the earliest Acheulean bifaces, where removals are limited (e.g. no greater than 12 at Kokiselei-4; Texier 2018).

Moreover, the limited intra-site variation at Gona (2.6 Ma) indicates that early Oldowan hominins already possessed a capacity for high-fidelity transmission, laying the foundations for a biocultural feedback process supporting the cumulative coevolution of lithic technology and hominin cognition (Stout et al. 2019; Tomasello 1999). This facilitated Oldowan innovations, including the *débitage* reorganisation and large flake production that are crucial for the Acheulean (Texier 2018; Wynn 2002). Organic tools may have also experienced developments given use-wear evidence for Oldowan woodworking (Lemorini et al. 2014, 2019). Shea (2010) conceptualizes early bifaces as allometric extensions of Oldowan cores, which may indicate that these traditions fall on a continuum of adaptive behavioural practices rather than discrete cognitive shifts.

In this paper, we propose that the technological continuum observed in East African Early Pleistocene assemblages can be explained by the extent of knowledge about the distribution and predictability of resources within specific landscapes. Palaeolithic technological investment may reflect a balance between landscape resource predictability and resource returns: increasing reliability in the outcome of resource procurement strategies allows for a greater investment in lithic technologies.

Landscape knowledge, dietary strategy and lithic technology

Primates inhabit specific but diverse landscapes in which populations must know the resource distribution patterns within their environment. This is a collective knowledge. For instance, chimpanzees (*Pan troglodytes*) differentially convey newly discovered information with nearby individuals (e.g. Brosnan and de Waal 2000). Social knowledge transmission facilitates the development and consolidation of population specific behaviours among chimpanzees such as nut-cracking (Boesch et al. 1994). This relationship between socially transmitted knowledge networks and dietary behaviours is paramount since, according to dietary breadth models, animals rank resources in their environment by their energetic reward (Kelly 2013). For example, captive chimpanzees use memory as a tool to sort retrieval of food sources distributed across their range by energy/handling time (Sayers and Menzel 2012). Wild populations can also incorporate their optimal exploitation time and feedback information about food patches to conspecifics (Janmaat et al. 2014; Kalan et al. 2015) and warn other group members about the presence of predators nearby (Schel et al. 2013). Thus, we can assume that the ability to socially accumulate knowledge of the environment is basal to the hominin lineage and an important dimension of early human survival strategies, representing the underlying mechanism for landscape habituation and technological variability (cf. Davis and Ashton 2019).

The accumulation of knowledge in these novel landscapes in the context of more open, arid and seasonal Early Pleistocene environments (Blumenthal et al. 2019; deMenocal 2004; Potts 2012; Vrba 1985) may have been underpinned by biological adaptations to variable environments (cf. Potts 1998). One such adaptation, obligate bipedalism, enlarged hominin home ranges (e.g. Antón et al. 2002; Foley 1992) allowing exploitation of increasingly distant and unevenly distributed resource patches (such as carcasses). This would require a reconfiguration of knowledge networks incorporating information about temporal changes to resource distribution and returns, how to maximize nutritional return in a given handling time and competition from con- and hetero-specifics, since even daylight plant gathering in open savannah ecosystems involves an increased encounter rate with large and potentially dangerous species (Lewis and Werdelin 2007).

The fact that hominins were able to navigate these landscapes and began to exploit increasingly patchy resources is illustrated by multiple examples of animal exploitation dating to the Early Pleistocene (de Heinzelin et al. 1999; Domínguez-Rodrigo et al. 2005a; Sahnouni et al. 2018). A co-evolutionary outcome of repeated meat and marrow consumption is that their high calorific return allowed for investment in cerebral development (e.g. Aiello and Wheeler 1995; Foley and Lee 1991). The available taphonomic evidence seems to suggest that many early episodes of marrow, meat and viscera consumption involved early access to animal carcasses. However, even if some remains were passively or confrontationally scavenged (Pobiner 2020), this active procurement represents a marked difference from animal consumption in other primates. For instance, chimpanzees tend only to scavenge carcasses attributable to hunting by conspecifics disregarding those left by carnivores, suggesting an inability to recognize certain species as potential food sources or toxin avoidance from decomposing carcasses (Watts 2008). Furthermore, since carcass sites are locales of active ecological interaction, even facultative scavengers are forced to assess the risk of accessing low-cost but highly sought-after nutrients to avoid unfavourable disputes (Lima and Bednekoff 1999; Luttbeg 2017; Palomares and Caro 1999; Wilson and Wolkovich 2011). Taken together, this early exploitation of animal remains reflects the required reconfiguration of knowledge networks when increasing inhabitation of savannah environments. This trend may have followed Pliocene developments in the opportunistic ability to take resources from larger (defleshed) carcasses (cf. Thompson et al. 2019).

Time-budget constraints imposed by movement between resource patches and procurement risks should emphasize selection for reduced handling costs of higher-ranked resources to maximize dietary return during restricted feeding time (Foley and Elton 1998). Adaptive lithic technologies can reduce handling costs of food resources as a function of resource density and predictability. If a resource is exploited opportunistically, investment in complex technologies is inefficient since dietary returns are uncertain. In contrast, a recurrent or predictably anticipated access to these resources will encourage a greater lithic investment as the incurred costs will be offset by increased dietary output per unit of processing time. Indeed, Binford (1979) notes that Nunamiut lithics produced in anticipation of future need throughout the environment were more structured than expedient technologies produced for an immediate need. We predict therefore, a pattern that emphasizes reactive processing upon discovery of immediate resource exploitation opportunities, with expedient flake production on local raw materials. Knapping should follow a method most suited to the nodule morphology and natural flaking angles to produce sharp flakes. These patterns may be associated with the simple unidirectional and unifacial schemes that predominate in many Oldowan sites (Gallotti 2018).

The development of knowledge networks reflects the interplay between tool complexity requirements, activity duration and threat levels. These networks facilitate predictable opportunities for exploitation of highly-ranked animal and plant resources with high acquisition and/or processing costs. In turn, this should be associated with a similarly predictable need for lithic technologies across the landscape (cf. Binford 1979; Kuhn 1995). The potential for high dietary returns therefore makes investment in raw material transport a worthwhile part of structured group activities across the landscape, with a corresponding increase in the diversification and standardization of lithic sequences reflecting the need to maximize the utility of transported raw material. This need not reflect an increase in settlement mobility but rather a more structured and wider-ranging engagement with the exploitable landscape. More complex and structured knapping strategies allow the production of a much greater number of flakes for the same volume of core for extended procedures, such as processing of wood and/or large animal carcasses. Secondary retouch represents another mode of diversifying the 'toolkit' for undertaking additional tasks (e.g. hide processing, defleshing and disarticulation). In this way, the production of tools such as scrapers, notches and denticulates would allow for optimal exploitation of aggregated resources in a minimized amount of time.

Taken together, our Landscape Knowledge Networks model (fig. 1) suggests that the complexity of lithic toolkits in the Early Pleistocene is intrinsically linked to the nature of resource procurement and subsistence strategies of a given hominin group, both of which rely on the development of suitable knowledge networks within a given environment. It is important to stress that different resource procurement strategies are not mutually exclusive. A flexible exploitation of complementary sources can mediate seasonal and yearly availability oscillations, thus allowing for greater predictability (DeVault et al. 2003; Pereira et al. 2014; Wilmers et al. 2003). We argue that it is precisely the combination of different strategies that can explain a large proportion of the technological variability in the archaeological record, including the Oldowan-Acheulean transition.

In the following sections, we apply this model to a subset of the archaeological record of the Oldowan and Early Acheulean in East Africa. Discussed sites

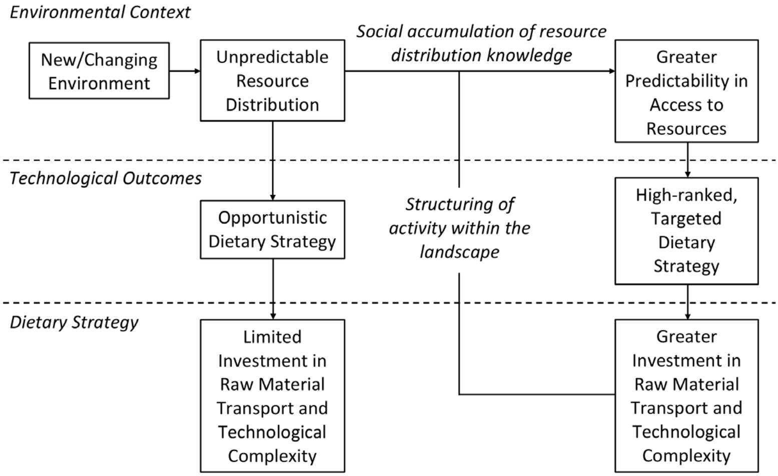

Figure 1 Schematic representation of the Landscape Knowledge Networks model for understanding and interpreting Early Pleistocene technological and behavioural variability in East Africa. Rather than assuming an irreversible and unidirectional trend, this model also allows for abrupt dynamic exits from the positive feedback loop due to changes in landscape resource distribution such as those associated with climate change or seasonality regimes as well as those derived from the colonization of new landscapes. While cognitive developments are not considered necessary for hominin populations to reach the right-hand side of the diagram, those with greater levels of socialization (particularly within later periods) may be able to accumulate knowledge of their environment at increasingly reduced timescales.

(fig. 2) exhibit diversity in lithic reduction schemes and most display a degree of faunal preservation that allows for an assessment of the correlation between lithic investment and dietary strategies. Nonetheless, some assemblages still lack a convincing demonstration that the observed relationships between bones and lithics are not merely palimpsests incorporating very different biotic and non-biotic processes (Domínguez-Rodrigo 2009). In other words, we cannot assume that hominins were directly and uniquely responsible for the co-occurrence of animal bones and stone tools in the same locality since fluvial and/or gravitational displacement as well as animal trampling and other natural processes can also juxtapose those elements in the archaeological record. Therefore, a thorough taphonomic analysis ought to be carried out before implying the role of hominin agency as the primary site formation process.

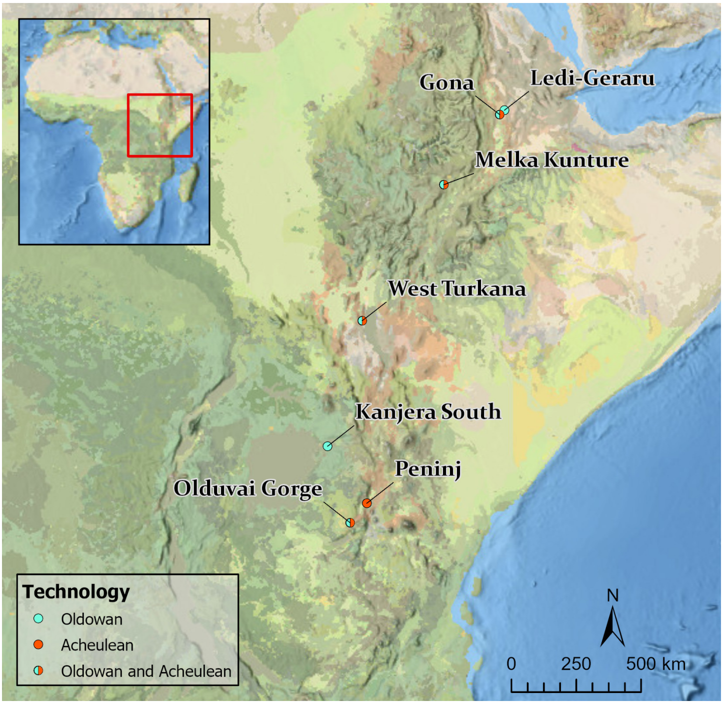

Figure 2 Map of East African archaeological localities discussed in the text. The presence of Oldowan assemblages is indicated in blue and Acheulean assemblages are indicated in red.

Development of landscape networks throughout the Oldowan

Our model suggests that technological adaptations occurred alongside increasing predictability in access to and reliance upon highly-ranked plant and animal resources. We do not expect uniform or unidirectional developments in flaking diversity through time across different landscapes since a key tenet of the model is that the cognitive capacity for shifts from simple to more complex flaking schemes would have been present from the beginning of the Early Pleistocene. However, we may expect a broad trend towards an increasing knapping diversity and a more targeted selection of more suitable raw materials, often involving greater transport distances unless high-quality raw materials are already in the local catchment area. Barsky et al. (2013) suggest an analogous trend amongst European Lower Palaeolithic assemblages with a trajectory from inter-assemblage variability towards intra-assemblage diversity reflecting regional selective pressures. Similarly, Gallotti (2018) sees two distinct Oldowan phases for which detailed technological information is available: an early phase 2.6–2.3 Ma, encompassing Gona, and a later phase 2.0–1.6 Ma, characterized by greater intra- and inter-site flaking variability, alongside increased raw material transport distances (Hovers 2012).

Nevertheless, flaking complexity is also demonstrated in early phases of the Oldowan such as at Gona c.2.6–2.5 Ma. This markedly seasonal palaeolandscape (Quade et al. 2004) comprises three major lithic assemblages in two distinct technological clusters (de Lumley et al. 2018; Semaw et al. 1997, 2003; Stout et al. 2010). The East Gona 10 and 12 (EG-10 and EG-12) assemblages, identified on a semi-arid floodplain, are dominated by the use of local raw materials such as trachyte and rhyolite, and core-reduction is biased towards unifacial flaking (59%). Ounda Gona South 7 (OGS-7; in a channel bank context) conversely shows a greater representation of bifacial and multi-facial cores (86%) produced on higher quality and selectively transported aphanitic and vitreous volcanic materials (Stout et al. 2010). We argue that the non-local material and reduction complexity at OGS-7 reflects an investment in the exploitation of predictable and recurrent resources while the expediency of EG-10 and EG-12 would represent less predictable seasonal resource acquisition strategies. Active monitoring of the East Gona floodplain sites as animals migrate to perennial water sources in the dry season (Pereira et al. 2014) may represent opportunistic exploitation of carrion pulses and/or instances of compensatory hunting, while OGS-7 could be associated with wet-season or potentially year-round exploitation of plant, animal and aquatic resources in the riverine context. While none of these sites preserve clear faunal associations, the taphonomy of the coeval nearby sites of EG-13 and OGS-6 respectively indicates primary access to animal remains (Domínguez-Rodrigo et al. 2005a). The environmental patterning of lithic assemblages at Gona supports the existence of embedded knowledge networks that afforded hominins spatio-temporal planning of activities across the landscape for extended periods of time.

The innovations of the later Oldowan phase are illustrated by Kanjera South (western Kenya), Kokiselei-5 (West Turkana, Kenya) and Garba IVE-F (Melka Kunture, Ethiopia). The hominins of Kokiselei-5 (1.87 Ma) developed the ability to create new striking platforms to reorganize *débitage* allowing them to control reduction in three dimensions (Texier 2018). This builds on the local innovation of cobble breakage sequences to generate initial knapping angles, as reconstructed from the relatively large refitting groups at Lokalelei-2C (Delagnes and Roche 2005; de Lumley et al. 2018). The access to high-quality obsidian at Garba IVE-F (1.7 Ma) facilitated systematic production of retouched tools (31% of obsidian flakes) for the first time in the Oldowan (Gallotti 2018; Gallotti and Mussi 2018a; Negash et al. 2006). Reduction of raw material is intensive, employing a diversity of schemes, primarily multi-facial, multi-directional (Gallotti and Mussi 2015, 2018a). In addition, while lithic and faunal distributions have been influenced by post-depositional processes, there is tentative evidence that bone remains are more strongly associated with obsidian material than the less elaborate basalt artefacts (D'Andrea et al. 2002).

Such associations between biotic resource exploitation and lithic technology are even clearer at Kanjera South (2 Ma). Here, reduction frequently follows intensive bifacial centripetal schemes, including on relatively large flakes (Braun et al. 2009) and 28% of the raw material was selectively transported more than 10km to the site (Braun et al. 2008). The assemblage is also associated with frequent processing of underground storage organs and herbaceous plant resources, woodworking activity and recurrent primary access to animal remains (Ferraro et al. 2013; Lemorini et al. 2014, 2019). This predictable access to a combination of different resources, at least some of which were highly ranked, would reflect the structuring of activities within the landscape and thus support investment in the lithic assemblage.

The non-linearity predicted by our model is illustrated by the lithic assemblages of Olduvai Gorge Bed I (~1.85–1.80 Ma, Tanzania). These assemblages show very little inter-site metrical variation with flakes frequently retaining cortex and most frequently produced by unifacial, followed by bifacial, reduction schemes (de la Torre and Mora 2005a, 2005b; Gallotti 2018; Leakey 1971). Raw material transport distances tend to be extremely short (less than 4km and usually closer to 2km), making use of lava stream cobbles and quartz/quartzites from the local Naibor Soit (Gallotti 2018). Besides, most Bed I sites show very tight spatial clustering deriving from water availability patterns within the Olduvai landscape (Ashley et al. 2009, 2010; Blumenschine et al. 2012; Domínguez-Rodrigo et al. 2010) since permanent water sources attracted physiologically-stressed herbivores during the dry season (Hawkes 2016; Pereira et al. 2014). These localities would offer early humans and other predators frequent but relatively unpredictable opportunities for compensatory hunting and facultative scavenging, a pattern which we argue could account for the consistently expedient nature of flake production at Olduvai Bed I sites.

Consistent with our model, there is evidence for increasing investment in lithic technology over time amongst the Oldowan assemblages of Olduvai. While raw material transport distances remained low due to the local availability of quality material, lower and middle Bed II evidence more frequent multi-facial reduction and structured core exploitation schemes as well as an increase in the frequency and diversity of secondarily retouched flakes (Proffitt 2018). While part of this trend may be explained by high quality chert becoming exposed as a result of the receding margins of the Olduvai palaeolake (de la Torre and Mora 2005a), these same trends are present on quartzite and, to a lesser extent, lava (Proffitt 2018). We suggest that Oldowan technological development at Olduvai is associated with an accumulation and consolidation of landscape knowledge which facilitated more predictable access to high ranking resources and warranted investment in the lithic assemblage.

The Acheulean: Detailed knowledge networks and structured use of the landscape

The African Acheulean is characterized by a diversity of large (usually bigger than 10cm) flake production methods as blanks for predominantly bifacial tool production, which would require a cumulative increase in social investment from the Oldowan tool-making learning process (Gallotti and Mussi 2018b; Isaac 1969; Shea 2010). Large flakes at Kokiselei 4 (1.76 Ma) derive from splitting large cobbles (Lepre et al. 2011; Texier 2018). Those from FLK-West (~1.7 Ma) were released from bi- and multi-facial exploitation of large cores that mirrors small- and medium-sized flake production (Diez-Martín et al. 2015; Sánchez-Yustos et al. 2017). Those from Garba-IVD (~1.6 Ma) required flaking surface preparation and volume management according to the discoid concept (Gallotti 2013; Gallotti and Mussi 2018a). These sites are also typologically variable with massive scrapers dominating the formal biface morphotypes at Garba-IVD compared to picks at Kokiselei-4 and FLK-West. The latter shows large variability that prevents assignment of many to formal categories (Diez-Martín et al. 2015; Gallotti and Mussi 2018a; Texier 2018). Cleavers, particularly important in the Large Flake Acheulean (cf. Sharon 2009), are also present at Konso-Gardula in this early phase (Beyene et al. 2013). This variability could be indicative of more than one independent origin for the Acheulean technocomplex in East Africa, potentially united by a predictable need for flakes across the landscape (Shea 2010). This landscape-mediated behavioural adaptability of relatively small and dispersed hominin populations is further evidenced by the frequent co-occurrence of bifaces with core-and-flake elements (e.g. at Gona; Semaw et al. 2020) and the 1.4 Ma hippopotamus bone handaxe at Konso-Gardula (Sano et al. 2020).

At Olduvai this coexistence is environmentally patterned within the same fluvial system, with Oldowan assemblages including HWK, HWK-E and HWK-EE associated with smaller and shallower braided channels than the FLK-West Acheulean, located by a single deeper wider channel (Uribelarrea et al. 2017). The taphonomic data from FLK-West levels four to six, with the greatest lithic densities (Diez-Martín et al. 2015), stresses anthropogenic input through the presence of percussion marks and cut-marks suggesting intensive carcass processing, including marrow-extraction, defleshing and disarticulation of medium and large-sized adult bovids (Yravedra et al. 2017). In contrast, the taphonomic signatures of both hominins and carnivores at HWK-EE (also ~1.7 Ma) indicate a high competition seasonal environment. While hominins prioritized the procurement of medium- and large-sized carcasses (cut marks on ~12% of NISP), the skeletal profiles exhibit a degree of density mediated preservation typical of secondary carnivore ravaging and more than 30% of NISP show carnivore damage (Pante and de la Torre 2018). The associated lithic assemblage shows very limited structured reduction occurring most frequently on relatively low-quality lava cobbles available in the immediate vicinity with very little flaking intensity or retouch (biased towards infrequent chert and quartzite flakes) and nearly all cores preserving some cortex (Pante and de la Torre 2018).

Rather than attributing the above mentioned Oldowan inter-assemblage differences to distinct hominin species (cf. Leakey 1971), we argue that this pattern would be consistent with a more predictable spatio-temporal distribution of animal and plant resources at FLK-West due to reliable water availability (Uribelarrea et al. 2017). This predictability would have supported investment in toolkit diversification for effective hunting and carcass processing. In contrast, the more expedient toolkit at HWK-EE alongside proficient butchery skills is consistent with the need for fast processing of carcasses upon discovery of procurement opportunities throughout the dry season (Pante et al. 2018; Rivals et al. 2018), when hominins could anticipate higher carnivore competition.

Peninj (Lake Natron, Tanzania; 1.7–1.4 Ma) attests to such an Early Acheulean structuring of the lithic record with activity throughout the landscape. The Peninj record is distributed between sites in the lacustrine environment of the Type Section and on the surrounding escarpments (Diez-Martín et al. 2018;

Domínguez-Rodrigo et al. 2005b) and the archaeological assemblages show notable differences in the toolkits associated with each area. Assemblages in the Type Section tend to lack bifaces (with exceptions) and instead show intensive exploitation of raw material (especially through discoid-like reduction of small-medium cores) alongside primary anthropogenic access to carcasses (Mora et al. 2003). In contrast, the sites of Noolchalai and Lepolosi on the escarpments show a fairly large biface assemblage with very similar technological schemes (Diez-Martín et al. 2018). They may be associated with woodworking (cf. Domínguez-Rodrigo et al. 2001) which could reflect investment in organic tools and/or even shelter infrastructure. Nonetheless, all sites are united by large flakes and biface rejuvenation flakes, suggesting that Peninj represents an interconnected regional Acheulean system shaped by the constraints and affordances of the landscape (Diez-Martín et al. 2018). Such a pattern is clearly consistent with the further expansion of embedded knowledge networks to facilitate predictable exploitation and spatial mapping of resource distribution.

Conclusions

The behaviour of Early Pleistocene human groups was directly related to the extent and plasticity of their embedded social knowledge of the landscape, combining an awareness of resource distribution patterns and the ability to successfully track and exploit those resources. We therefore offer an interpretive framework that can explain and illustrate the broad scale behavioural differences present in Early Pleistocene assemblages. Technological variation may stem from these population dependent processes as such networks facilitate a capacity for foreplanning concrete spatio-temporal interactions with the environment to ensure predictable access to highly ranked resources.

We suggest that expedient flaking schemes in the Early Pleistocene, particularly in the Oldowan, are associated with relatively unpredictable exploitation of tool requiring resources, most easily demonstrable through the exploitation of carcasses resulting from natural deaths or compensatory hunting of vulnerable individuals during the dry season, when overall food availability is lower. Lithic investment does allow for higher returns by reducing resource handling costs, but the overall returns will not compensate for the increased processing costs unless the resource is predictably available and recurrently procured. Hominins would have also had access to resources that did not require flaked stone tools to process (fruits, honey, insects, etc.) and as such their exploitation predictability would not be reflected in the archaeological record.

Knowledge accumulation through long-term landscape habituation (Davis and Ashton 2019) would accommodate spatio-temporal fluctuations in highly-ranked resource distribution patterns and densities. We associate this foreplanning with greater raw material transport distances and an associated intensification and diversification of reduction to maximize return from the investment in raw material. Thus, we interpret the Acheulean as a continuation of Oldowan-emerging trends, with technological innovation related to increasingly developed landscape knowledge networks and the explicit targeting of seasonally-specific and/or year-round resource patches.

Finally, we argue that this Early Pleistocene behavioural flexibility, through an ability to accumulate landscape knowledge, facilitated expansion into novel ecosystems beyond the range of previous hominins. Nonetheless, such long-distance movements would necessarily have disrupted ongoing habituation to the source environment, while also potentially rendering obsolete any previous landscape-specific information about the ranking and spatio-temporal distribution of resources. We therefore associate these dispersals with a subsequent reconfiguration of landscape knowledge networks and a shift towards a broader set of lower-ranked food resources and a more generalized lithic toolkit, in the context of more opportunistic resource exploitation strategies.

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