

Seasonality and Oldowan behavioral variability in East Africa

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Abstract

The extent, nature, and temporality of early hominin food procurement strategies has been subject to extensive debate. In this paper, we examine evidence for the seasonal scheduling of resource procurement and technological investment in the Oldowan, starting with an evaluation of the seasonal signature of USOs, freshwater resources, and terrestrial animal resources in extant primates and modern human hunter-gatherer populations. Subsequently, we use the mortality profiles, taxonomic composition, and taphonomy of the bovid assemblages at Kanjera South (Homa Peninsula, Kenya) and FLK-Zinj (Olduvai Gorge, Tanzania) to illustrate the behavioral flexibility of Oldowan hominins, who were targeting different seasonally-vulnerable demographics. In terms of the lithic assemblages, the specific opportunities and constraints afforded by dry season subsistence at FLK-Zinj may have disincentivized lithic investment, resulting in a more expedient toolkit for fast and effective carcass processing. This may have been reinforced by raw material site provisioning during a relatively prolonged seasonal occupation, reducing pressures on the reduction and curation of lithic implements. In contrast, wet season plant

abundance would have offered a predictable set of high-quality resources associated with low levels of competition and reduced search times, in the context of perhaps greater seasonal mobility and consequently shorter occupations. These factors appear to have fostered technological investment to reduce resource handling costs at Kanjera South, facilitated by more consistent net returns and enhanced planning of lithic deployment throughout the landscape. We subsequently discuss the seasonality of freshwater resources in Oldowan procurement strategies, focusing on FwJj20 (Koobi Fora, Kenya). While more analytical studies with representative sample sizes are needed, we argue that inter-assemblage differences evidence the ability of Oldowan hominins to adapt to seasonal constraints and opportunities in resource exploitation.

Keywords: Seasonality; Zooarcheology; Taphonomy; Lithic technology; Early Pleistocene; Oldowan.

1. Introduction

The Oldowan represents the first geographically and temporally widespread lithic tradition of the African Early Stone Age, and can be characterized by the removal of sharp (often short and thick) flakes from cores by direct percussion, with little secondary modification (Gallotti, 2018; Shea, 2020). Assemblages of this nature first appear around the beginning of the Early Pleistocene (~2.6–2.5 Ma) at Ledi-Geraru and Gona, Ethiopia (Semaw et al., 1997; Semaw et al., 2003; Braun et al., 2019). Their appearance is correlated with a period of major climatic change in East Africa (Plummer, 2004), as the gradual onset of the Northern Hemisphere Glaciation, particularly around ~3.0–2.6 Ma, resulted in demonstrably cooler and more variable worldwide climates (e.g., Lisiecki and Raymo 2005; Herbert et al., 2010; Joordens et al., 2019; Trauth et al. 2021). In Africa, this process may have involved an expansion of grasslands and turnovers in mammalian faunas (e.g., Vrba, 1985; deMenocal, 1995; Bobe and Behrensmeyer, 2004; deMenocal, 2004; Cerling et al., 2011; Potts, 2012; Potts and Faith, 2015), but these are likely to have been gradual and regionally-distinct (Trauth et al., 2021). An important consequence of these changes is the evidence for an intensification of yearly seasonality to levels comparable to the modern-day by at least 2 Ma (Blumenthal et al., 2019).

In many regions of East Africa, these patterns would imply the alternation of dry and wet seasons, which can be identified directly at paleolake basin sites with intra-annual fluctuations in water level, such as Olduvai Gorge (Beverly et al., 2014). Butzer (1982) argued that the strategic location of hominin sites in mosaic environments with access to different resource patches would have mediated the seasonal fluctuation of water and resources, with sites in the African interior restricted to wetter climatic phases. In contrast, Speth (1987) proposed that the increasing seasonality associated with the Plio-Pleistocene transition would have had crucial implications for

hominin ecological fitness, requiring the development of adaptive subsistence strategies able to successfully cope with the cyclical resource stress inherent to the food supply mechanisms of hunter-gatherer and primate communities living in semi-arid landscapes. Ethnographic and primatological studies attest to the notion that seasonal fluctuations in resource availability and quality in subtropical environments have a considerable influence on the food-procurement strategies and dietary composition of both modern human hunter-gatherers and non-human primates (e.g., Speth, 1987; Hawkes et al., 1989; Marlowe and Berbesque, 2009; Lee, 2013; Oelze et al., 2014). Recent approaches are showing that such seasonal variations also influenced hominin diets (e.g., Sponheimer et al., 2005; Sponheimer et al., 2006; Joannes-Boyau et al., 2019).

Resource availability is not the only factor to consider for understanding the optimality of hominin foraging strategies (cf., Hawkes et al., 1982; Foley, 1985; Kurland and Beckerman, 1985; Ferraro, 2007). For example, even when an attractive resource is available in a given season, a minimum level of landscape knowledge may be required for their consumption. Clark and Linares-Matás (2020) define landscape knowledge as the extent to which a population is aware of the distribution and predictability of specific resources within their unique habitat, suggesting that this information determines the extent of engagement and technological investment in their exploitation. This may explain why chimpanzees (*Pan troglodytes*) at Lopé Reserve, Gabon, do not partake in nut-cracking, despite the bioavailability of nuts and the existence of suitable raw materials (McGrew et al., 1997).

From the perspective of dietary breadth models, animals rank resources in their environment by their nutritional rewards relative to search, procurement, and processing costs (Stephens and Krebs, 1986; Kelly, 2013). Both high- and low-ranked plant and other non-mammalian resources are likely to have been very important to hominin diets throughout human evolution, given their

considerable contributions to primate and hunter-gatherer diets (Tanaka, 1976; Goodall, 1986; Hawkes et al., 1989; Hawkes et al., 1995; Kitanishi, 1995; Marlowe and Berbesque, 2009; Melin et al., 2014). Meat and within-bone resources, such as marrow, have a particularly high calorific and nutritional potential (e.g., Bunn and Ezzo, 1993; Cordain et al., 2001; Tennie et al., 2009), and thus are likely to have been an attractive resource for Early Pleistocene hominins. Evidence for animal exploitation is often the best preserved direct evidence of Early Pleistocene subsistence, with the appearance of the Oldowan penecontemporaneous with the first secure evidence for hominin processing of animal remains¹. This pattern is first documented at Gona and Bouri, Ethiopia around 2.6–2.5 Ma (de Heinzelin et al., 1999; Domínguez-Rodrigo et al., 2005), and at Ain Boucherit, Algeria, from 2.4 Ma (Sahnouni et al., 2018). Lithics are likely to represent an adaptation for a faster and more efficient processing of particular resources available to hominins, including the manufacture of organic implements (e.g., Isaac, 1986; Toth, 1987; Plummer, 2004; Domínguez-Rodrigo et al., 2009; Gürbüz and Lycett, 2021).

Since certain primate genera are known to sporadically consume animal resources (Stanford, 2001; Surbeck and Hohmann, 2008; Watts, 2020), occasional omnivory was likely a basal hominin trait (Stanford, 2012; Wood and Gilby, 2017). Nonetheless, meat is still a relatively marginal dietary component in bonobos (*Pan paniscus*; Oelze et al., 2011), while chimpanzees only rarely approach even the lowest levels of meat consumption seen in tropical hunter-gatherer societies (Watts, 2020). Therefore, it is likely that several shifts towards greater emphasis on animal consumption took place during the course of hominin evolution (Speth, 1989; Foley, 2001; Bunn, 2007; Domínguez-Rodrigo and Pickering, 2017; Thompson et al., 2019; Pobiner, 2020). This

¹ The earliest reported cut-marks in the archaeological record derive from Dikika, Ethiopia, from 3.39 Ma (McPherron et al., 2010), but their identification has been contested on taphonomic grounds (e.g., Domínguez-Rodrigo and Alcalá, 2016).

101 increasing reliance on higher-quality resources may have driven brain growth and physiological
102 development (cf., Foley and Lee, 1991; Aiello and Wheeler, 1995). Resource provision may also
103 have influenced the life history strategies of hominins (e.g., Hawkes et al., 1997), facilitating the
104 required ontogenetic patterns for the development of increased neural complexity (cf., Hawkes and
105 Finlay, 2018).

106 We argue that seasonality is a critical framework for understanding hominin resource
107 procurement strategies in the Early Pleistocene of East Africa, as recently explored by Hosfield
108 (2020) in relation to the European Lower Paleolithic. In this paper, we first provide an overview
109 of the seasonal scheduling of resource consumption in relation to fluctuations in availability and
110 nutritional returns, with a view to generating hypotheses about the archaeological record. We
111 subsequently apply these insights to Oldowan subsistence strategies at Kanjera South and FLK-
112 Zinj, two crucial sites for understanding the nature of hominin access to animal resources (Bunn
113 and Pickering, 2010; Domínguez-Rodrigo et al., 2010; Blumenshine et al., 2012; Ferraro et al.,
114 2013; Parkinson, 2013; Parkinson, 2018; Oliver et al., 2019). We argue that seasonal changes in
115 subsistence patterns and habitat selection would have profound implications for the predictability
116 of resource distributions across the landscape and their dietary returns, influencing the nature of
117 both food-procurement strategies and technological investment. We also discuss the seasonal
118 relevance of freshwater resources at Oldowan sites, particularly FwJj20, in terms of both their
119 potential contribution to hominin diets and as important paleoecological indicators.

2. Seasonal resource availability and food procurement preferences in tropical and subtropical environments

There are a number of resources with seasonal fluctuations in availability which may have been exploited by hominins, such as honey, insects (including colonial and soft-bodied invertebrates), fruits and berries, roots and tubers, freshwater taxa, and terrestrial animal resources (e.g., Bunn et al., 1988; Stewart, 1994; Sato et al., 2012; Lesnik, 2014; Marlowe et al., 2014; Melin et al., 2014). Indeed, use-wear data on early bone technology from multiple South African Early Pleistocene sites indicate extractive foraging through termite fishing or digging for roots and tubers (Backwell and d'Errico, 2001; d'Errico and Backwell, 2009; Stammers et al., 2018). Here, we focus our review on the importance for hominins of three resource types in particular: underground storage organs (USOs), freshwater taxa, and terrestrial animal resources.

The consumption of terrestrial USOs, including roots and tubers, is relatively common among certain chimpanzee communities, such as those of Ugalla and the Mahale Mountains, Tanzania, during the wet season (Hernandez-Aguilar et al., 2007; Yoshikawa and Ogawa, 2015). At Ugalla, this constitutes a period of low fruit availability (Hernandez-Aguilar et al., 2007). This wet season bias for terrestrial USO consumption is also documented among human foragers in tropical and subtropical environments, such as the Hiwi of the Venezuelan Amazon (Hurtado and Hill 1990) and the Baka of southeastern Cameroon (Sato et al., 2012). This pattern may be linked to lower procurement costs when the soil is softer, since the ground hardens during the dry season and becomes more difficult to penetrate in certain environments (e.g., the savanna of Ugalla; Hernandez-Aguilar et al., 2007). These acquisition costs may help to explain why the Aka of northeastern Congo show lowest tuber exploitation in the late dry season, despite this being the period where tubers are at their greatest size and return potential (Kitanishi, 1995). Among the

Hadza of northern Tanzania, tubers may be brought to the camp in greatest quantities during the wet season (Vincent, 1985; Marlowe and Berbesque, 2009), but procurement is fundamentally a year-round foraging activity, with the number of foraging trips dependent on the seasonal availability of preferred berries (Hawkes et al., 1989; Hawkes et al., 1995; Marlowe and Berbesque, 2009). This pattern highlights that when higher-ranked resources have tightly-constrained seasonal signatures, there is a need to adaptively schedule the consumption of different resources to maintain nutritional quality throughout the year (Laden and Wrangham, 2005; Lambert, 2007; Marshall and Wrangham, 2007; Marshall et al., 2009).

Freshwater fish represent one such seasonally-constrained but nutritious food source that carnivores and non-human primates occasionally exploit (Turnbull-Kemp, 1967; Goodall, 1971; Ewer, 1973; Kruuk, 1976; Hamilton and Tilson, 1985; Russon et al., 2014). Freshwater resources are often an important source of essential polyunsaturated fatty acids and proteins for tropical and subtropical hunter-gatherers, potentially playing an important role in human evolution (Broadhurst et al., 2002; Jerardino and Marean, 2010; Joordens et al., 2014; Kyriacou et al., 2016). Consumption of such resources may have emerged in the context of seasonal exploitation of USOs, sedges, seedless vascular plants, and aquatic macrophytes in mosaic riparian environments (Sept, 1984; Wrangham et al., 2009; Stewart, 2010; Magill et al., 2016). For example, aquatic USOs (which are not subject to the same soil hardness constraints as terrestrial USOs) are exploited by yellow baboons (*Papio cynocephalus*), to the greatest extent during the dry season, when preferred foods are scarce (Wrangham et al., 2009). The transition between the late dry and early wet seasons is a particularly productive period in these environments for opportunistic human fishing (cf., Dufour, 1987; Sato et al., 2012). This is underpinned by a requirement for cognitive mapping of seasonal fluctuations in water bodies, and knowledge requirements pertaining to specific seasonal

fish behaviors in their habitual watercourses. In Eastern Africa, the late dry season is associated with migratory catfish (*Clarias* spp.) and nesting Cichlidae becoming trapped and exposed in shallow receding ponds (Leakey, 1971). In the early wet season, large quantities of catfish then migrate upriver during the early rains to spawn (Greenwood, 1955), and some perciforms, including cichlids, construct their nests in the shallows of river floodplains and lakes (Stewart, 1994). Since cichlids are very territorial, African fisher communities of the Bangwelu Wetlands of northeastern Zambia often make spatial references on their recurrent nesting areas to ensure successful fishing encounters during the wet season (Brelsford, 1946). Thus, fish could have been a seasonally predictable and relatively easy to catch prey for Oldowan groups if they were able to become acquainted with the location and fluctuations of seasonal lakes and streams.

On the other hand, primates and hunter-gatherer or fisher-forager groups also have the opportunity to target certain freshwater resources, such as turtles, shellfish or migratory fish, during the wider wet season, albeit at variable acquisition costs. Isolated instances of targeted wet season acquisition of fish and crabs in shallow, slow-flowing waters have been documented among long-tailed macaques (*Macaca fascicularis*) in Indonesia (Son, 2003; Stewart et al., 2008). Among the Hiwi hunter-gatherers of Venezuela, the capture of freshwater turtles is predominantly carried out during the late wet season, focused on the stable waters of oxbow lakes alongside river courses (Hurtado and Hill, 1990). Indeed, a heavy wet-season bias in chelonid exploitation relative to ungulate hunting by Kalahari San groups was used by Speth and Davis (1976) in one of the first attempts to infer the seasonality of selected Early Pleistocene sites in East Africa.

Terrestrial animal resources present another dietary category particularly relevant to discussions of the Early Pleistocene archeological record. There is much evidence for a seasonal signature in chimpanzee hunting behaviors, but the same patterns are not consistently repeated

between sites in different ecological settings (Mitani and Watts, 2005). Of particular relevance to hominin behavior, chimpanzee hunting in open savanna environments focuses on the acquisition of small vertebrates with low individual return rates (Pruetz et al., 2015; Moore et al., 2017). In contrast, however, the targeting of larger animal carcasses is observed consistently within the hominin lineage from the Early Pleistocene (Domínguez-Rodrigo et al., 2005; Braun et al., 2010; Bunn and Pickering, 2010; Ferraro et al., 2013; Parkinson, 2018). As such, seasonal patterns of meat availability and/or preference in modern human hunter-gatherers may provide clearer insights about the intra-annual patterning of Oldowan food procurement strategies.

In the diets of many modern tropical and subtropical hunter-gatherer populations, animal resources play a relevant role year-round, although meat consumption tends to be most frequent during the dry season. For example, among the Baka, and the Mbuti of the Ituri Forest (northeastern Congo), dry season procurement of mammals is consistently greater than during the wet season (Ichikawa, 1983; Sato et al., 2012). Similarly, the greatest period of meat consumption in the Hadza also occurs in the dry season, reaching ~40% of food brought back to camp by weight in the late dry, and dropping to as little as ~10% during the early wet (Marlowe and Berbesque, 2009). Among the Ju/'hoansi, Botswana, this general pattern is replicated, with meat also observed to provide up to 80% of the diet during two months of one particularly severe dry season, when all other resources were rather scarce (Weissner and N!aici, 1998; Lee, 2013). This pattern is likely to result from the interplay between changes to overall resource abundance and to resource quality and ranking by season.

The reduction of plant availability and the evaporation of rain-fed seasonal watercourses during the dry season in arid and semi-arid regions of Africa often leads to the concentration of weakened herbivores around the few permanent water sources still present in the landscape, as

these animals require access to forage persisting around these areas as well as drinking water to compensate for the dehydration of plant foods (Thrash et al., 1995; Redfern et al., 2003; Chamaille-Jammes et al., 2008; Valeix 2011). This spatial clustering of hunting and scavenging opportunities ensures that predators do not need to spend as much time searching for prey in the dry season, and have a greater success rate in locating them (Bunn et al., 1988; Hurtado and Hill, 1990; Foley, 1993; O’Connell et al., 2002; Hawkes, 2016). These animal resources also have a greater dietary return than most individual available plants, which further encourages a shift towards their procurement (Pobiner, 2015). This ecological pattern can help explain why most meat tends to be consumed by the Hadza and other subtropical hunter-gatherers during the dry season, providing a greater dietary contribution in the face of seasonal and inter-annual fluctuations in plant resource availability (Vincent, 1985; Bunn et al., 1988; Hitchcock, 1989; Hawkes et al., 1991; O’Connell et al., 1992; Hawkes et al., 1997; Sherry and Marlowe, 2006; Marlowe and Berbesque, 2009; Lee, 2013).

At the same time, modern human populations have a limit for protein consumption of around 30–40% of dietary calories, with consumption above this threshold exceeding the body’s ability to metabolize urea (Cordain et al., 2000). As a result, repeated consumption of lean meat results in a breach of the ‘protein ceiling’—which may lead to protein poisoning—thus placing relatively tight constraints on its consumption and rendering it an ineffective resource under food stress conditions (Binford, 1978; Speth, 1983; Cordain et al., 2000). Indeed, a pattern of fat-depleted animal avoidance is documented among hunters in semi-arid environments, who may even abandon whole carcasses if they are too lean (Tindale, 1972; Hayden, 1981; Speth, 1983). In a similar fashion, contemporary African fishers may throw fat-depleted fish back to the water (Brelsford, 1946; Jubb, 1967).

In contexts of marginal nutritional intake, fat and especially carbohydrates, have a protein-sparing effect, as the body is also able to derive energy from these non-protein sources, thus reducing the metabolic demands associated with amino acid catabolism (Munro, 1964; Richardson et al., 1979; Speth and Spielmann, 1983; Bunn and Ezzo, 1993). During periods of fat-depletion in animal carcasses, Cordain et al. (2000) suggest that hunter-gatherers must either show a preferential selection for fattier individuals or carcass portions, hunt larger animals with greater proportions of body fat, or increase their consumption of plant resources, particularly those with high carbohydrate concentrations. A general preferential selection of fattier animals is reported by many different hunter-gatherer groups across different ecosystems (Tomita, 1966; Hart and Hart, 1986; O'Dea et al., 1991). In particular, the hunting of different duiker (*Cephalophus* spp.) species predominantly during the dry season by the Mbuti corresponds to the only period of the year when these animals store substantial mesentery fat, as reflected in high kidney fat index (KFI) values (Ichikawa, 1983; Hart and Hart, 1986). Similarly, Lee (2013) reports that the Ju/'hoansi make their first cut of an ungulate carcass along the breastbone, in order to first check the extent of subcutaneous fat, and gain access to the viscera. This preference for fatty body parts is even a common finding among chimpanzees (e.g., Boesch and Boesch, 1989; Pruetz et al., 2015). For example, Gilby and Wawrzyniak (2018) report that chimpanzee consumption of primate prey at Gombe follows a predictable pattern based on immediate returns, in which energy-dense, fat-rich resources, such as viscerae and head-contents, were usually exploited first. This body of evidence strongly suggests that one of the main attractions of animal carcasses for human and non-human primates is fat-rich tissue (Hayden, 1981; Hill et al., 1984; Lee, 2013). Therefore, the interplay between physiological constraints and prey selection strategies makes body fat fluctuation a

critical aspect for modelling seasonal patterns of terrestrial ungulate consumption in the Early Pleistocene (Speth, 1987; Bunn and Ezzo, 1993; Cordain et al., 2000; Ben-Dor et al., 2011).

As the dry season advances, the reduction in the quality and distribution of food resources leads to declines in body fat percentage among terrestrial ungulates (Speth, 1987). In modern African savannas, ungulates try to mitigate these trends through the deployment of seasonal dietary and mobility strategies that play a considerable role in regulating their abundance and population dynamics (Staver and Hempson, 2020). Ungulates of the Serengeti ecosystem (northern Tanzania) tend to subsist on sub-maintenance diets for most of the dry season, using the consumption of large amounts of low-quality forage as a way to slow the rate of utilization of their internal fat reserves (Sinclair, 1975). This pattern leads to a time lag between the point of lowest total caloric intake and the point of poorest condition (i.e., nutritional yield) of African ungulates (Sinclair, 1975; Speth, 1983). Total carcass fat is therefore at its lowest around the end of the dry season and the beginning of the rainy season (Speth, 1987).

This time lag in ungulate physiology therefore has paramount implications for understanding the impact of seasonal food stress on Oldowan animal food procurement strategies, since it implies that the quality of animal resources will have declined less rapidly than that of plant resources in the dry season (Bunn and Ezzo, 1993). As such, we expect hominin consumption of meat resources to be greater during most of the dry season, excluding the very late dry. In the early wet season, ungulate carcasses would still exhibit a high degree of fat-depletion. Moreover, terrestrial ungulates tend to disperse in the face of wider plant biomass availability with the onset of the rains, resulting in lower encounter rates. At this time of the year, hominins should have therefore preferentially targeted carbohydrate-rich resources (berries, honey, and tubers), and energy-dense fatty resources, such as freshwater species or the brains, viscerae, and marrow of terrestrial

280 ungulates, alongside any protein intake (Table 1). Towards the second half of the wet season, we
 281 would expect animal carcasses to regain their overall nutritional attractiveness, although their
 282 dispersed pattern would entail higher search costs.

Resource		Seasonal Preferences			References
		Dry season	Very late dry to early wet transition	Wet season	
Underground storage organs (USOs)	Terrestrial	Moderate	Moderate	High	Hawkes et al. (1989, 1995); Kitanishi (1995); Hernandez-Aguilar et al. (2007); Marlowe and Berbesque (2009); Sato et al. (2012)
	Aquatic	High	Moderate	Low	Laden and Wrangham (2005); Wrangham et al. (2009); Stewart (2010)
Freshwater resources		Low	High	Moderate	Leakey (1971); Speth and Davis (1976); Stewart (1994)
Terrestrial animal resources	Meat and marrow	High	Low	Moderate	Sinclair (1975); Speth and Davis (1976); Blumenschine (1987); Bunn et al. (1988); Blumenschine and Madrigal (1993); Bunn and Ezzo (1993)
	Viscerae and head contents	Moderate	High	Moderate	Bunn and Ezzo (1993); Speth and Spielmann (1983); Cordain et al. (2000); Gilby and Wawrzyniak (2018)

283 **Table 1:** Hypothesized seasonal preferences (based on resource availability, constraints, and
 284 returns) for the main set of resources discussed in the text for Oldowan hominins.

285 Lastly, we recognize the additional importance of inter-annual differences in the magnitude
 286 of fluctuations in resource quality and availability, and that these changes may limit our ability to
 287 confidently infer seasonality (e.g., Hawkes et al., 1991; Speth et al., 1991). Nonetheless, we
 288 propose that the intra-annual framework outlined here can still be broadly applied to the
 289 characterization of hominin adaptation to recurrent terrestrial animal resource variability, with
 290 seasonality being a key driver of this pattern at the yearly scale.

3. Carcass acquisition strategies by Oldowan hominins

3.1. *Hunting versus scavenging debate*

Early paleoanthropological research was quick to take for granted that hunting was a quintessential activity of early *Homo*, driving their socio-economic and technological organization (cf., Lee and DeVore, 1968). Glynn Isaac's (1978; Isaac, 1984) work contributed to the shift of emphasis towards the underlying social organization, structured through cooperation, a gendered division of labor, and the subsequent sharing of food resources at home bases. This period also witnessed the first detailed zooarcheological and taphonomic research on Early Pleistocene faunal remains as sources of evidence (Behrensmeyer, 1978; Bunn et al., 1980; Binford, 1981; Bunn, 1981; Potts and Shipman, 1981). When Binford (1985) analyzed skeletal part profiles and superficially assessed the nature of bone surface modifications at FLK-Zinj, he concluded that hominins appeared to have been marginal scavengers of carnivore kills. This interpretation fostered actualistic research assessing whether hominin exploitation of abandoned carnivore kills could have represented a reliable source of nutrients (Blumenschine, 1986; Blumenschine, 1987; Blumenschine, 1988; Domínguez-Rodrigo, 1994; Domínguez-Rodrigo, 1999; Pobiner, 2015). However, subsequent taphonomic and actualistic research amongst modern hunter-gatherers highlighted the relevance of an abundant representation of high-yielding skeletal parts bearing anthropogenic modifications, such as cut-marks and percussion marks, for identifying stone-tool mediated butchery at FLK-Zinj and Koobi Fora sites (e.g., Bunn, 1986; Bunn and Kroll, 1986; Shipman, 1986; Bunn et al., 1988; O'Connell et al., 1988a; O'Connell et al., 1992).

The interpretation of the abundance, anatomical distribution, and overlap between bone surface modifications (cut-marks, percussion marks, and carnivore tooth marks) on mammal bones became the next major avenue of taphonomic and actualistic research (Blumenschine et al., 1994;

Domínguez-Rodrigo, 1994; Domínguez-Rodrigo, 2001). Several researchers have concluded that the tooth mark and percussion marks counts reported by Blumenschine et al. (1994) for FLK-Zinj fit a carnivore-hominin-carnivore model—whereby hominins scavenged carcasses abandoned by large felids, with bones subsequently ravaged by hyenids (Blumenschine, 1995; Capaldo, 1997; Pante et al., 2015). Nonetheless, a considerable proportion of the tooth-marks reported in Blumenschine et al. (1994) have been subsequently reassessed as having a natural biochemical origin unrelated to carnivore activity (Domínguez-Rodrigo and Barba, 2006; Parkinson, 2018). The pattern resulting from the new tooth mark estimates better fits Blumenschine's hammerstone-to-carnivore model, indicating primary access of hominins to carcasses, either by hunting or confrontational scavenging, followed by secondary carnivore scavenging (Domínguez-Rodrigo and Barba, 2006). This revision is also more consistent with the anatomical placement and frequency of cut-marks and percussion marks (Bunn and Kroll, 1986; Bunn and Ezzo, 1993; Parkinson, 2013; Parkinson, 2018). Early access to carcasses following a hominin-first model has also been reported for other Oldowan sites, including DS (Olduvai Bed I; Cobo-Sánchez, 2020) and Kanjera South (Ferraro et al., 2013; Parkinson, 2013), and can therefore be considered a relevant feature of Early Pleistocene hominin dietary behaviors.

At the same time, portraying early hominin carcass acquisition as an either/or dichotomy between the hunting of prime game and the scavenging of carnivore leftovers is likely misplaced (cf., Bunn and Kroll, 1986; Blumenschine, 1987; Potts, 1988). Indeed, insights from carnivore ethology suggest that most predators engage to an extent in both hunting and opportunistic scavenging by adaptively responding to seasonal fluctuations in prey distribution, prey body condition, and carrion availability, with the selected strategy reflecting an ecological trade-off between energetic investment and dietary output (Molinari-Jobin et al., 2004; Owen-Smith, 2008;

Pereira et al., 2014; Mattison et al., 2016). The Hadza provide a hunter-gatherer example of this phenomenon, as individuals are able to respond quickly to scavenging opportunities, including passive scavenging of within-bone nutrients, when they appear at localities where they actively capture ungulate prey (Bunn et al., 1988; O’Connell et al., 1988b; O’Connell et al., 2002; Hawkes, 2016). We suggest that Oldowan hominins were also likely to have displayed the flexibility required to switch between different carcass acquisition and processing strategies (Speth, 1983; Bunn and Ezzo, 1993), particularly when facilitated by the deployment of lithic technologies (Foley, 1985; Ferraro, 2007).

3.2. Seasonality, prey selection, and carcass acquisition strategies

There are several possible methods of acquiring animal carcasses: scavenging the remains of animals that have died naturally or through predation (passive scavenging), ‘kleptoparasitism’ (confrontational/power scavenging) whereby predators are actively chased away from their kills, ‘compensatory/cursorial predation’ of individuals already vulnerable to death due to age or disease, and ‘additive predation’ of healthy individuals (Schaller and Lowther, 1969; Schaller, 1972; Pereira et al., 2014). These strategies are summarized in Table 2 (passive scavenging has been divided into facultative scavenging—feeding on earlier predator kills—and scavenging of natural death pulses), alongside their respective ecological patterning and archeological signatures as a framework for evaluating Pleistocene sites. We recognize that these discrete categories actually fall along an overlapping behavioral continuum of carcass acquisition behavior, and therefore hominins are likely to have employed these strategies at different points in time and in varying frequencies, depending on the potential returns, costs, and constraints in a given context.

Seasonality has a profound influence on these decision variables, due to changes in factors such as soil condition, maximum daily temperature, cloud cover, precipitation, animal physiological condition, and prey densities. A wide range of carnivores and human-hunter-gatherers adopt compensatory prey selection strategies that are intrinsically linked to these predictable intra-annual changes. For example, lions (*Panthera leo*) of Hwange National Park, Zimbabwe, preferentially target buffalo (*Syncerus caffer*) year-round, but males show an increase in the hunting of vulnerable juveniles when they become more abundant during the wet season (Davidson et al., 2013). Furthermore, lions opportunistically exploited a range of other seasonally-vulnerable animals, including juvenile elephants taken during very late dry season droughts (Davidson et al., 2013). Leopards (*Panthera pardus*) also actively adapt their prey selection strategies to take advantage of birthing seasons and ecosystem changes (Karanth and Sunquist, 1995; Yang et al., 2018).

Bunn and Ezzo (1993) argued that a flexible adoption of carcass procurement strategies based on intra-annual body condition variability could have provided hominins with a suitable supply of animal resources at different points of the year. Ethnographic accounts of hunting strategies by San groups in the Kalahari demonstrate a pattern of seasonally-vulnerable ungulate prey selection, targeting animals more prone to tiredness on the basis of attributes that fluctuate over different temporal scales such as reproductive status, age, injury, illness, hunger, or thirst. For example, !Xo and G/wi hunters of the Kalahari choose to pursue certain Bovidae, such as steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and gemsbok (*Oryx gazella*), during the rainy season, when the wet sand forces open their hoofs and stiffens the joints (Schapera, 1930; Liebenberg, 2006). In the dry season, Kalahari hunters prefer to track greater kudu (*Tragelaphus strepsiceros*), eland (*Taurotragus oryx*), and red hartebeest (*Alcelaphus caama*)

males with heavy horns or pregnant females, who become exhausted faster when running on loose sand (Liebenberg 2006). In each case, the hunters identify and follow trails of isolated weaker individuals, who are exhausted and have splintered from the rest of the herd to hide in the bush (Liebenberg, 2006).

The nature and temporality of carcass acquisition strategies determine the specific animal nutrients and skeletal parts available to Oldowan hominins at any given site (Schaller and Lowther, 1969; Bunn and Ezzo, 1993). We can predict a focus on high-ranking (and fatty) viscerae whenever hominins had primary access to the carcass (e.g., Lee 2013; Gilby and Wawrzyniak, 2018), most clearly documented through cut-marks on the ventral side of ribs (cf., Nilsson, 2000). This would have been particularly important to hominins during seasonal fat-depletion in terrestrial ungulate carcasses (very late dry to early wet transition), where meat itself becomes very lean. Other elements with high fat availability that are often left by large felids, such as head contents or the marrow of limb bones (Pobiner, 2015), are likely to have been favored whenever available, regardless of the timing of access to the carcass (Thompson et al., 2019). This pattern may have been exacerbated seasonally, with focus shifting towards bones that retain the greatest overall amounts of fat, such as the tibiae, or those which deplete more slowly, such as the lower limb bones (Newlin and McCay, 1948; Turner, 1979; Speth, 1987; Speth, 1990; Blumenschine and Madrigal, 1993).

Strategy	Trophic engagement	Access to carcass	Returns	Procurement costs	Planning requirements	Mortality profiles	Taphonomic signature	Relevant Oldowan references
Facultative scavenging	Passive	Secondary	Meat scraps and within-bone nutrients	Low: late access to carcasses reduces initial competition	Low	Representative of primary carnivore(s)	Abundant tooth-marks Cut-marks on low-ranking parts	Binford (1981); Blumenschine (1987); Pante et al. (2012)
Scavenging of natural death pulses	Passive	Primary	Multiple whole carcasses Poor physiological condition	Low-Intermediate: competition can be high	Low-Intermediate: predictable carrion pulses	Attritional, occasionally catastrophic	Mass nearby concentration of natural deaths Emphasis on evisceration and within-heads contents	Capaldo and Peters (1995); Lam (2008)
Confrontational scavenging	Passive	Early	Near-complete carcasses	Intermediate: involves carnivore encounters	Intermediate: anticipation of carnivore behavior and chasing away	Representative of primary carnivore(s)	Low evisceration cut-mark counts High-incidence of defleshing cut-marks	Medium to large carcasses: Bunn and Ezzo (1993); Bunn (2001); O'Connell et al. (2002)
Compensatory hunting	Active	Primary	Complete carcasses	High	High	Seasonally vulnerable demographics	Evisceration and defleshing cut-marks	Small Carcasses: Bunn and Pickering (2010); Oliver et al. (2019)
Additive hunting	Active	Primary	Complete carcasses	Highest	Highest	Prime adults	Evisceration and defleshing cut-marks	Medium to large carcasses: Bunn and Pickering (2010); Bunn and Gurtov (2014)

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Table 2: Profile of different possible carcass acquisition strategies available to Oldowan hominins. Procurement costs include those incurred while procuring the carcass, its processing, and its defense.

The availability of certain terrestrial animal nutrients and skeletal parts to Early Pleistocene hominins would have nonetheless been partially reliant on the carcass acquisition strategies followed (Table 2). Thus we can predict an initial focus on viscerae, whenever hominins had primary access to the carcass, as well as the head contents and within-bone nutrients of skeletal elements with high marrow contents at that time (such as the tibiae) and/or those with delayed depletion (such as the lower limb bones), regardless of carcass acquisition strategy (Newlin and McCay, 1948; Turner, 1979; Speth, 1987; Speth, 1990; Blumenschine and Madrigal, 1993). As such, we hypothesize that dry season Oldowan sites may show a greater dependence on animal tissue, with most parts of the carcass (including meat) providing an attractive resource (cf., Blumenschine, 1987; Bunn et al., 1988; Bunn and Ezzo, 1993). On the other hand, during periods of greatest ungulate physiological stress (most commonly the very late dry season and the early wet season), we would expect to see an increased emphasis on skeletal parts that retain the greatest proportions of fatty nutrients (cf., Cordain et al., 2000). For example, the fat contents of brain and viscerae, particularly the liver, remain relatively constant throughout the year, while adipose tissue mass and bone marrow gradually become depleted under conditions of nutritional stress (Cordain et al., 2002; Kuipers et al., 2010). Nonetheless, the marrow of distal appendicular bones, particularly metapodials—which contain the highest proportion of digestible low-melting-point fatty acids—tends to become depleted last among ungulates (Speth, 1987; Blumenschine and Madrigal, 1993).

4. Seasonally-mediated behavioral variability at Kanjera South and FLK-Zinj

Carcass acquisition strategies at Early Pleistocene sites are frequently assessed taphonomically, but limited faunal preservation or a lack of a clear association with co-occurring lithic assemblages often prevent an accurate assessment of hominin behavior (Domínguez-Rodrigo, 2009). Nonetheless, it may be possible to demonstrate a relationship between resource exploitation strategies, seasonality, and the nature of lithic assemblages at certain Oldowan sites, such as Kanjera South, Kenya (2.0 Ma), and FLK-Zinj (FLK Level 22), Olduvai Gorge, Tanzania (1.84 Ma; Bunn, 1981; Bunn and Ezzo, 1993; de la Torre and Mora, 2005; Braun et al., 2009b; Domínguez-Rodrigo, 2009; Ferraro et al., 2013; Parkinson, 2013; Oliver et al., 2019; Figure 1).

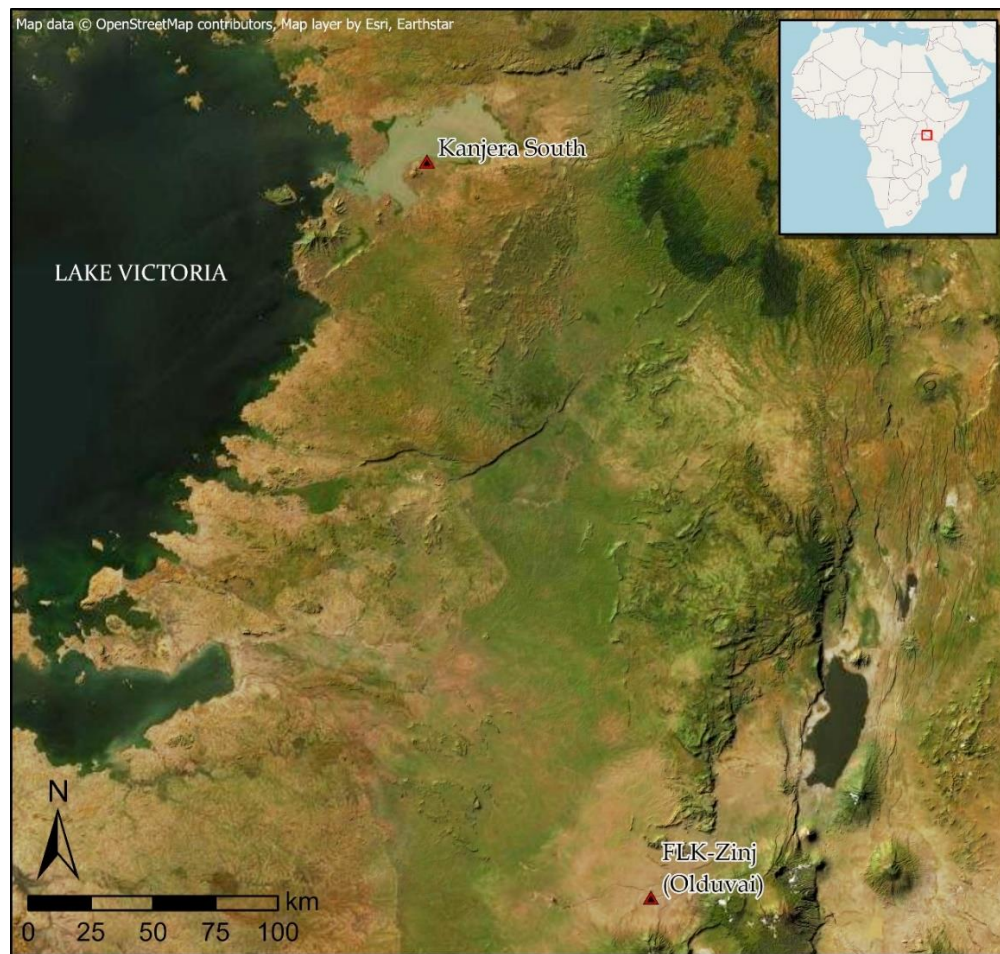


Figure 1. Map depicting the location of FLK-Zinj and Kanjera South, the two main Oldowan case-studies discussed in the paper.

In terms of the lithic assemblages, Kanjera South frequently evidences bifacial centripetal schemes, including on relatively large flakes, while 28% of the raw materials exploited were selectively transported >10 km from conglomerates in the neighboring Awach drainage basin (Braun et al., 2008; Braun et al., 2009a; Braun et al., 2009b). This may also be reflected in the underrepresentation of cores in relation to flakes at the site, suggesting cores were transported into the site for flake production, and then removed from the site for future use (Plummer and Bishop, 2016). Unidirectional unifacial methods were often restricted to local fenitized Nyanzian rhyolites or dacites and Homa limestone or phonolite of poorer quality (Braun et al., 2009a; Reeves et al., 2021), with transported materials being more heavily worked, and were selected according to the durability of their cutting edge over flaking predictability (Braun et al., 2009a; Braun et al., 2009b; Reeves et al., 2021). Flakes from these non-local raw materials also occasionally display secondary retouch, something that is extremely rare for the Oldowan (Plummer and Bishop, 2016; Gallotti, 2018). These patterns of relatively long-distance transport and elongated reduction sequences are suggestive of a considerable planning of activity across the landscape, potentially related to predictability of resource exploitation.

In contrast, the FLK-Zinj lithic assemblage is characterized by unidirectional and unifacial reduction on local quartzite raw materials, resulting in a greater impression of expediency than Kanjera South (Leakey, 1971; de la Torre and Mora, 2005; Braun et al., 2009a; Gallotti, 2018). Immediately local lava (particularly basalt) cobbles are abundant in Leakey's (1971) unmodified 'manuport' assemblage, but represent a much smaller proportion of exploited cores, suggesting a preference for the quartzite material (de la Torre and Mora, 2005). This pattern suggests selection for cutting ability over durability (Key et al., 2020). Retouched flakes are also very rare, despite flakes and flake fragments representing the focus of the assemblage (Leakey, 1971; de la Torre

and Mora, 2005; Gallotti, 2018). Taken together, the raw material transport distances at FLK-Zinj, similar to many other Olduvai Bed I sites (Gallotti, 2018), hint at a directional movement into the Olduvai paleolandscape via an appropriate raw material source (i.e. Naibor Soit).

The taphonomic evidence from the faunal assemblages, which we discuss in more detail below, suggests that hominins had primary access to carcasses at both Kanjera South and FLK-Zinj (e.g., Bunn, 1981; Domínguez-Rodrigo, 2009; Bunn and Pickering, 2010; Ferraro et al., 2013; Parkinson, 2013; but see Pante et al., 2012). However, we would argue that paleoecological and taphonomic data illustrate differences in the nature and seasonality of resource procurement strategies between Kanjera South and FLK-Zinj.

4.1. Kanjera South

The site of Kanjera South (western Kenya) is centrally located within the northern margins of the alluvial fans that cover the carbonatite geology of the Homa Peninsula, by the shore of Winam Gulf, Lake Victoria (Behrensmeyer et al., 1995; Plummer et al., 1999; Plummer and Bishop, 2016). The presence of lithic and faunal remains in the colluvial and alluvial silts and sands of beds KS1–3 has been dated to 2.30–1.92 Ma through magneto- and bio-stratigraphy (Ditchfield et al., 2019). The gentle nature of the deposition and the high sedimentation rates at the lake margin, as suggested by minimal bone weathering and absence of both fluvial rounding and debris-flow accumulations, favored the good preservation of archeological remains (Ditchfield et al., 2019). The primary context of the site is further reinforced by the existence of several artifact refits and the diversity of skeletal parts with differing water transport potential (Plummer et al., 2009; Parkinson, 2013). The recurrent sedimentation cycles have afforded researchers an opportunity to explore the nature of Oldowan hominin behavior through the time-lapse represented

in the KS1–3 beds, since humans were the primary biotic agent responsible for the accumulation of archeological materials (Ferraro et al., 2013). Another interesting paleoecological component of the Kanjera ecosystem is the predominance of open C₄ grassland habitats, alongside some indications of woodland/grassland ecotones and a permanent watercourse, as inferred from the $\delta^{13}\text{C}$ values of soil carbonates and herbivore enamel (Plummer et al., 2009). This existence of nearby watercourses is reinforced by the presence of water-dependent taxa, such as hippotamids, crocodilians, and reduncine bovids, although they are relatively rare in the sequence (Oliver et al., 2019). The stability of resource exploitation strategies throughout the three archeological levels at Kanjera South attests to the consistently productive nature of the landscape and repeated seasonal attraction of the site over hundreds or even thousands of years (Ferraro et al., 2013; Lemorini et al., 2014; Ditchfield et al., 2019).

In terms of zooarcheological data, the Kanjera South assemblage shows an even representation of skeletal part profiles for small bovids (e.g., *Antidorcas* sp., *Gazella granti*), which indicates procurement and processing of whole carcasses. In relation to the mortality profiles, dental eruption and epiphyseal fusion rates suggest that a high proportion (50%) of both size 1–2 and size 3 bovids were young or subadult at the time of death (Parkinson, 2013; Plummer and Bishop, 2016; Oliver et al., 2019; Table 3). The anatomical distribution of bone surface modifications indicates that hominins had early access to the small prey size carcasses (Parkinson, 2013). The presence of cut-marks on small bovid remains, such as a metatarsal (KJS 7472) or the proximal epiphysis of a femur (KJS 2565), is associated with limb disarticulation (Ferraro et al., 2013), with the restricted intensity and frequency of carnivore damage indicating an only occasional incidence of secondary scavenging (Parkinson 2013; Plummer and Bishop 2016). This aligns well with the conclusions of Oliver et al. (2019) that the accumulation of size 1–2 bovids in

the Kanjera South assemblage results from a hominin strategy of hunting vulnerable juvenile individuals, which granted them complete and early primary access.

Bovid category	Young juveniles	Subadult juveniles	Prime adults	Old adult	Total MNI
Small bovids (sizes 1–2)	7 (31.8%)	4 (18.2%)	8 (36.4%)	3 (13.6%)	22
Larger bovids (sizes 3a/3b)	8 (20.0%)	12 (30.0%)	18 (45.0%)	2 (5.0%)	40

Abbreviations: MNI = minimum number of individuals.

Table 3: Bovid mortality profiles from Kanjera South, in terms of MNI (%). Data derived from Oliver et al. (2019: Table 2).

We can better understand the seasonal relevance of the Kanjera South mortality profiles by using analogues derived from extant bovid ecology (Foley, 1983). The temporality and synchronicity of African bovid births are considerably variable, based on the timing of food supply growth (in relation to both protein peak and overall biomass), the length of time food is available, and anti-predator behavior exhibited (Jarman, 1974; Rutberg, 1987; Ims, 1990; Sinclair et al., 2000; Kingdon, 2015). According to Sinclair et al. (2000), most small bovid species living in small groups with non-precocial calves give birth during the wet season, although they do not exhibit a high degree of birth synchronicity. *Gazella* spp. for example, tend to produce their young early in the wet season, ahead of the high protein peak (Sinclair et al., 2000). In contrast, bovids living in larger herds with precocial young tend to have more tightly synchronized birth periods (Sinclair et al., 2000). Of particular relevance to the Kanjera South zooarcheological assemblage—where Alcelaphini (3a) play an important role (Ferraro et al. 2013; Oliver et al. 2019)—topi (*Damaliscus lunatus*) births also tend to peak around the onset of the wet season (Sinclair et al., 2000). As such, the number of juveniles from a range of bovid species is likely to peak during the wet season

(Pereira et al., 2014; Kingdon, 2015). This abundance makes them a paramount seasonal resource that is most frequently exploited by omnivorous, rather than obligate, carnivores (Pereira et al., 2014).

Small African antelope species, such as *Gazella* spp. and dik-dik (*Madoqua* spp.), follow a ‘hider’ strategy (cf., Jarman, 1974), through which mothers conceal their calves rather efficiently in the tall grass, out of sight from stalking cheetahs and other predators (Murdock et al., 1983; Ralls et al., 1986; FitzGibbon, 1993). However, hominins would have been able to overcome these anti-predator strategies and turn them into a predictable source of compensatory hunting opportunities by investing time into learning how to track the maternal vocalizations of gazelles prior to their daily feeding instances (Lent, 1974). This knowledge would, in turn, reveal the location of vulnerable nursing juveniles to the hominin groups that were actively monitoring the behavior of these species (cf., Oliver et al., 2019). Gaining access to small bovid calves could have provided hominins with a mechanism to attract and capture adult females as well: recent observations of Hadza hunting practices documented how a hunter deliberately distressed a recently-captured kudu calf so it would call its mother for help (Corey, 2021). On the basis of prey ethology, we argue that the active human hunting of juvenile bovids in the grassland environment of Kanjera South evidences hominin presence during at least the early-mid wet season at the site. Such a seasonal pattern would be consistent with observations of wet season Hadza hunting patterns (Hawkes and O’Connell, pers. comm.), the relatively low levels of carnivore competition documented at the site (Parkinson, 2013), and the paleoecological relevance attributed to seasonally moist soils and ephemeral streams (Ditchfield et al., 2019). At the same time, more analytical data is needed to confirm the season of death of ungulates acquired at the site, with research into bovid tooth microwear patterns underway (T. Plummer and J. Oliver, pers. comm.).

If a pattern of broadly wet season ecology holds for the wider occupation of Kanjera South, we would predict hominins to be preferentially targeting fat-rich animal products when available, while also focusing on abundant and accessible plant resources, such as USOs.

Such a preference for fatty resources may be hinted at in the exploitation of larger ungulates in the Kanjera South faunal assemblage. In comparison to the smaller bovid size classes, the mortality profiles for size 3 bovids at Kanjera South are still biased towards young and sub-adult individuals (see Table 3 above), although they show an increase in the proportion of prime-aged individuals with regards to the minimum number of individuals (MNI; Oliver et al., 2019). This pattern has been suggested to be representative of a combined strategy of compensatory hunting of younger individuals as well as the scavenging of carcasses from other carnivore kills (Oliver et al., 2019). The zooarcheological evidence for the medium-large bovid assemblage at Kanjera exhibits an uneven skeletal part representation that reflects a weight-minimizing carcass transport strategy (Ferraro et al., 2013). Selective body part transport should reflect an attempt to maximise net nutritional returns, although the overrepresentation of bovid crania and mandibles at Kanjera South, differs from usual patterns documented among the Hadza and other hunter-gatherers (Binford, 1978; Bunn et al., 1988; O'Connell et al., 1988a; O'Connell et al., 1990; Metcalfe and Barlow, 1992; O'Connell et al., 1992; Schoville and Otárola-Castillo 2014). We speculate this deviation may be a consequence of a) a potentially greater reliance on passive scavenging when acquiring cranial remains, resulting in reduced access to the yields of other body parts, and/or b) that ethnographic observations of carcass acquisition and transport often take place in the dry season, which may not account for seasonal fluctuations in the nutritional quality of different body parts. In this context, marked asymmetries in skeletal part profiles of prime-aged individuals in the Kanjera medium-large bovid assemblage—potentially derived from overlapping and very

different acquisition and butchery events (cf., Lupo, 2001)—may also skew the overall MNI patterns away from juvenile specimens, which still represent 50% of individuals in this bovid size class (Table 3).

The taphonomic signatures of post-cranial remains of medium-large bovids highlight the presence of cut-marks on ribs and limb bones, occurring alongside a limited number of carnivore tooth marks (Ferraro et al., 2013; Parkinson, 2013). This taphonomic pattern indicates that hominins had access to viscera and highly-prized cuts of meat. These body parts are usually consumed quickly by lions and other carnivores following a kill (O’Connell et al., 1988b; Domínguez-Rodrigo, 1999). This pattern would suggest that the role of primary carcass acquisition methods in the formation of the post-cranial faunal assemblage was quite considerable, perhaps resembling more closely the pattern of hunting young and subadult individuals suggested by Oliver et al. (2019) for the smaller bovid size class. A recent comparative multivariate discriminant analysis of Oldowan mortality patterns further indicates that Kanjera South hominins had early access to medium-sized bovids (Cobo-Sánchez, 2020).

With regards to post-cranial within-bone nutrients, Parkinson (2013) notes that percussion marks in the entire bovid assemblage are predominantly found on tibiae (c.40%)—the highest-ranked bone for marrow extraction in terms of calorific output (Blumenschine and Madrigal, 1993)—while their overall count across all main long limb bones is low ($n = 15/6\%$, consistent with the 6–9% values on midshaft fragments reported by Ferraro et al., 2013). This pattern of low percussion mark counts despite high bone fragmentation might have been caused by a breakage pattern in which hominins broke the bones against an anvil (Oliver, 1992; Parkinson, 2013). Nonetheless, the low emphasis on within-bone nutrients of limb bones at the site may have also been related to the seasonal temporality of marrow fat depletion (Sinclair, 1975; Speth, 1987;

Speth et al., 1991). In this context, we also note that the proportion of midshafts with percussion marking increases with bovid size class in the KJS-1 and KJS-2 units (Parkinson, 2013). This pattern is consistent with observations that larger animals preserve increased quantities of fat for longer during periods of nutritional depletion (Cordain et al., 2000).

The overabundance of isolated cranial and mandibular remains seems to suggest a preferential transport of these elements to the site, with the presence of clear percussion striae confirming that hominins targeted the consumption of their contents (Ferraro et al., 2013). The excess cranial elements in proportion to post-cranial MNI counts may imply a different procurement strategy, perhaps involving some extent of scavenging on skeletal parts left untouched by primary predators (Ferraro et al., 2013; Oliver et al., 2019). Alternatively, their presence may reflect the selective exploitation of natural deaths derived from late dry season carrion pulses, and/or the hunting of these animals primarily to target their crania and mandibles before an early abandonment of the rest of the fat-depleted carcass. Regardless, the procurement and exploitation of cranial remains would be consistent with an attempt to maximize consumption of fatty and energy-dense animal resources, such as brain matter and the mandibular nerve and/or marrow (Blumenschine, 1987; Speth, 1987; Cordain et al., 2000; Ferraro et al., 2013). Since fatty brain tissue contains one of the lowest protein percentages of any animal tissue (Jayathilakan et al., 2012), their consumption would have assisted Kanjera South hominins in avoiding the ‘protein ceiling’. The behavioral patterns inferred for the hominins at Kanjera South can be integrated into a coherent animal exploitation strategy using insights from observations of modern hunter-gatherers. In their ethnoarcheological study of a Kua rainy season camp (//oabe I)—occupied by 14 people for 7 nights—Bartram et al. (1991) noted that all nine ungulates procured were juvenile or neonatal, easily obtained once their hiding places were located, and the juvenile carcasses were

brought back whole to the camp. Furthermore, the Kua processed the skulls at the site to extract the brains and cranial pulps (Bartram et al., 1991). The acquisition of younger complete carcasses, alongside the larger bovid skulls, may have provided the Kanjera hominins with a similar opportunity to intensively exploit fat resources from younger carcasses and to obtain fat-rich material from both the complete juveniles and isolated skulls, including the fatty cranial matter.

As well as the evidence for the targeting of fatty animal resources, there is evidence for the exploitation of non-animal resources at Kanjera South. Indeed, use-wear analysis of the lithics reveals that, while around a third of tools were associated with butchery, the majority show signs of use related to the processing of medium-hard plant material, including wood and USOs (Lemorini et al., 2014; Lemorini et al., 2019). The processing and consumption of USOs at Kanjera South may match our predictions that they were a seasonally-relevant resource for hominins during times of reduced preferred food availability, such as when terrestrial ungulates are dispersed and/or fat-depleted (e.g., Speth, 1987; Laden and Wrangham, 2005; Hernandez-Aguilar et al., 2007; Marlowe and Berbesque, 2009; Wrangham et al., 2009; Sato et al., 2012).

The use-wear data also highlight a preferential use of non-local quartzites and rhyolites in plant processing, with the four analyzed retouched flakes of these materials showing evidence of cutting and scraping activities on medium-hard surfaces. At least three of these flakes were used on wood or hard herbaceous plants (Lemorini et al., 2014; Lemorini et al., 2019). This use-wear evidence for wood processing may be related to the production of organic tools, potentially including digging sticks for the extraction of USOs and hunting spears (Lemorini et al., 2014; Lemorini et al., 2019). Chimpanzees are known to use a diverse set of manufactured wooden tools, predominantly during the (early) wet season, for these purposes (Hernandez-Aguilar et al., 2007; Pruetz and Bertolani, 2007; Wynn et al., 2011), as well as for colonial invertebrate fishing

(McGrew et al., 1979; Goodall, 1986; Stewart and Piel, 2014; Hicks et al., 2019; Pascual-Garrido and Almeida-Warren, 2021). The Hadza also use wooden digging sticks to access USOs (Vincent, 1985). While preservation of wood is rare in the archeological record, recent finds from Gantangqing, China, indicate that hominins in subtropical environments were (seasonally) manufacturing such pointed implements and using them to obtain USOs, at least by the Late Middle Pleistocene (Gao et al., 2021). Investment in the production of wooden implements at Kanjera South is consistent with an attempt to minimize acquisition and processing costs of a desirable and predictable resource to maximize return yields (Ferraro, 2007; Clark and Linares-Matás, 2020). Although similar use-wear analyses at other sites are required for comparative purposes, we suggest that plant resource exploitation at this site may have played a greater role in governing the intensive exploitation of raw materials and the movement of lithics throughout the landscape than is conventionally discussed in the Oldowan literature.

4.2 FLK-Zinj

Frida Leakey Korongo-Zinjanthropus (FLK-Zinj) is a site located in Olduvai Gorge, Tanzania, situated within a very tight geographic cluster with most of Mary Leakey's (1971) sites in the Upper Member of Bed I. This pattern may be coincidental, or a reflection of specific features of the Olduvai landscape which were particularly attractive for the subsistence activities of hominins and carnivores (Domínguez-Rodrigo et al., 2010). Indeed, paleogeographic reconstruction of the Olduvai landscape emphasizes the presence of a saline-alkaline lake and a perennial freshwater spring, the latter of which lies very close to the known cluster of Bed I sites (Ashley et al., 2010; Domínguez-Rodrigo et al., 2010; Blumenschine et al., 2012). The presence of the perennial spring amidst lower lake levels fostered the development of a biodiverse

freshwater wetland at Olduvai (Ashley et al., 2009; Ashley et al., 2010; Domínguez-Rodrigo et al., 2010). This ecological setting would have been extremely attractive to dehydrated herbivores throughout the dry season—and by extension to hominins and carnivores, due to both their needs for drinking water and the opportunities for the active procurement of prey (Speth and Davis, 1976; Domínguez-Rodrigo et al., 2010; Hawkes, 2016; Domínguez-Rodrigo et al., 2019a).

On the basis of paleoecological reconstructions, the location of FLK-Zinj, on a topographical elevation by the edge of a lake floodplain, may have enjoyed a mosaic woodland vegetation pattern which could have offered hominins some degree of protection from carnivores (Ashley et al., 2010; Blumenschine et al., 2012; Uribelarrea et al., 2014; Arráiz et al., 2017). The skeletal part profiles of the site show a diverse taxonomic composition and near-complete representation of skeletal parts, although with an underrepresentation of the axial skeleton. Bunn (1986) suggests the high proportion of cranial remains and long bones suggests selective transport of high-ranking body parts into the site, whereas Blumenschine (1991) suggested that the pattern could reflect hominin transport of skeletal remains from scavenged carnivore kills. Other authors have suggested that the underrepresentation of axial elements and the limited evidence for disarticulation at FLK-Zinj derives from processes resulting in density-mediated differential preservation, such as secondary carnivore ravaging (Marean et al., 1992). From this perspective, near-complete carcasses would have been originally transported to the site from procurement spots located relatively short distances away (O’Connell et al., 2002; Faith et al., 2009; Domínguez-Rodrigo et al., 2010). Some degree of carcass transport towards a more sheltered spot mitigated carnivore competition at FLK-Zinj, evidenced by the presence of tooth marks on bovids and even on at least one hominin individual, bearing crocodile and leopard tooth marks (Domínguez-Rodrigo et al., 2010; Blumenschine et al., 2012; Njau and Blumenschine, 2012; Egeland, 2014; Aramendi et al., 2017).

While most Bed I lithic assemblages are associated with fauna of initial carnivore origin (Domínguez-Rodrigo et al., 2007), the functional association of lithics and faunal remains at FLK-Zinj is reinforced by taphonomic evidence suggesting hominins had primary access to the carcasses (e.g., Bunn, 1981; Domínguez-Rodrigo, 1997; Domínguez-Rodrigo and Barba, 2006; Parkinson, 2018). These factors indicate that carcass procurement and processing were co-occurring spatially at FLK-Zinj (Domínguez-Rodrigo and Cobo-Sánchez, 2017). Nonetheless, there is debate as to whether the dense concentrations of lithic artifacts and exploited faunal remains during the accumulation of the sedimentary unit at this focal point for hominin activity reflects prolonged occupations (e.g., Ashley et al., 2010), or a series of brief but recurrent visits limited to feeding (e.g., Blumenschine et al., 2012) within an extremely productive environment.

The taxonomic composition of the FLK-Zinj anthropogenic faunal assemblage mostly reflects local, non-migratory species, such as *Kobus*, *Antidorcas*, and *Parmularius* (Domínguez-Rodrigo et al., 2019b). Springbok (*Antidorcas* sp.) dominates the small-medium (size 1–2) assemblage, while waterbuck (*Kobus* sp.) is the most common amongst the size 3 bovids (Bunn and Pickering, 2010). Nowadays, migratory taxa (i.e., wildebeest [*Connochaetes gnou*]) are present in the Olduvai landscape mostly during the short wet season (Domínguez-Rodrigo et al., 2019b), although resident subpopulations may remain in the region year-round. Thus, if these actualistic patterns are relevant for understanding Early Pleistocene paleoecological patterns, the underrepresentation of migratory taxa would primarily suggest a dry season occupation (Domínguez-Rodrigo et al., 2019a). Models of calorific return from the marrow of different long bones at FLK-Zinj suggest that the exploited animals had suffered only very limited fat depletion (Blumenschine and Madrigal, 1993). This observation would also be consistent with a broadly dry season occupation.

While sample sizes are currently small, meso-wear and micro-wear patterns on ungulate teeth from the site suggest that the anthropogenic components of the FLK-Zinj assemblage likely formed during a single seasonal occupation, in contrast to the carnivore-accumulated Olduvai assemblage of FLK-N, which reflects more prolonged periods of carcass acquisition throughout the year (Domínguez-Rodrigo et al., 2019b). The tooth wear pattern could also represent repeated occupations in the same season over time, but the limited subaerial weathering documented on bone surfaces is more suggestive of relatively rapid sedimentary deposition (Domínguez-Rodrigo et al., 2007; Domínguez-Rodrigo et al., 2019b). Waterbuck teeth, the best-represented size 3 bovid at the site, exhibit a microwear pattern consistent with a mixed feeding diet (Domínguez-Rodrigo et al., 2019b). This pattern would better fit the dry season dietary preferences of waterbuck, since reduncines tend to follow a predominantly grazer regime during the wet season (Child and Richter, 1969; Herbert, 1972; Spinage, 1982; Gagnon and Chew, 2000; Kassa et al., 2007). Assuming FLK-Zinj was indeed primarily occupied during the dry season, we suggest that procurement of terrestrial animal resources, including meat, should represent an important part of the dietary strategy at the site.

The mortality profiles of size 1 and 2 bovids at FLK-Zinj are old-dominated (5/7, 71%; Bunn and Pickering 2010; Table 4). This pattern differs from leopard ambush hunting strategies, mostly focused on prime adults, meaning it is unlikely that size 1 and 2 bovids were confrontationally scavenged (Bunn and Pickering, 2010). Furthermore, primary hominin access is inferred taphonomically on the basis of the distribution of cut-marks on the high meat-yielding proximal and intermediate limb bones, complemented by the presence of percussion marks for marrow extraction, particularly on the tibiae (Parkinson, 2018). Early access is also supported by the nature of tooth mark density distribution on the tibiae and other hindlimb bones, which closely resembles

an experimental model in which the carnivore access follows hominin hammerstone use (Parkinson, 2018). Taken together, we would argue that the age profile seen amongst the small-medium bovids at FLK-Zinj is most consistent with compensatory hunting of vulnerable individuals.

Bovid category	Young juveniles	Subadult juveniles	Early prime adults	Late prime adults	Old adults	Total MNI
Smaller bovids (sizes 1–2)	0 (0.0%)	1 (14.3%)	1 (14.3%)	0 (0.0%)	5 (71.4%)	7
Larger bovids (sizes 3a/3b/4)	2 (10.0%)	4 (20.0%)	8 (40.0%)	4 (20.0%)	2 (10.0%)	20
Waterbuck (<i>Kobus sigmoidalis</i>)	2 (22.2%)	0 (0.0%)	3 (33.3%)	4 (44.4%)	0 (0.0%)	9

Abbreviations: MNI = minimum number of individuals.

Table 4: Bovid mortality profiles from FLK-Zinj, in terms of MNI (%). Data derived from Bunn and Pickering (2010: Table 1).

Large bovid procurement strategies at FLK Zinj have been variously interpreted as evidence of selective ambush hunting (e.g., Bunn and Pickering, 2010; Domínguez-Rodrigo and Pickering, 2017), non-selective (living structure), ambush hunting resembling Hadza and Kua practices (Bunn and Gurtoy, 2014), passive scavenging of felid-exploited carcasses (e.g., Blumenschine et al., 2012; Pante et al., 2015), confrontational scavenging of carnivore kills (e.g., Bunn, 2001; Bunn, 2007; O'Connell et al., 2002), or exploitation of carrion pulses (Capaldo and Peters, 1995; Lim, 2008). These strategies have also been evaluated with taphonomic evidence for hominin engagement with the carcasses, as well as the mortality profiles of the large bovid remains. With regards to the latter, the age profiles reported by Bunn and Pickering (2010) show a predominance of prime-aged individuals (12/20; 60%), with the proportion increasing to 77.8% (7/9) for waterbuck (*Kobus sigmoidalis*, size 3b).

Carrion pulses due to natural mortality are common towards the end of the dry season, when large herbivores are most likely to succumb to severe physiological stress (Sinclair et al., 2003; Pereira et al., 2014). However, they are unlikely to have provided extensive amounts of edible meat for hominins at FLK-Zinj, since these carcasses would be severely fat-depleted and thus not metabolically profitable (Speth, 1987; Blumenschine, 1987). Moreover, the mortality profiles at the site, especially the underrepresentation of old-age individuals, are substantially different to modern mass death events (Bunn and Gurtov, 2014). This is supported by systematic sampling carried out by The Olduvai Palaeoanthropology and Palaeoecology Project (TOPPP), which did not document large quantities of carcasses near the perennial spring at the time of FLK-Zinj occupation. This suggests that the hominin presence in the landscape was not coeval with any sizable carrion pulse (Domínguez-Rodrigo et al., 2010).

The proposal of a marginal and passive interaction with exploited and abandoned carnivore kills is undermined by evidence for recurrent early hominin access to the flesh of these medium/large animals (e.g., Domínguez-Rodrigo et al., 2007; Parkinson, 2013). Both femora and radio-ulnae show dense clusters of cut-marks in ‘hot zones’ (cf., Domínguez-Rodrigo, 1999), demonstrating that hominins had primary access to fleshed carcasses (Oliver, 1994; Parkinson, 2018). Confrontational scavenging has been proposed as one way of reconciling evidence for primary access without implying hominin hunting, since carnivore kills were a recurrent feature of the Olduvai Bed I paleolandscape (Bunn and Kroll, 1986; Bunn, 2001; O’Connell et al., 2002) and carnivore predation is a major source of mortality for medium-sized ungulates in the Serengeti (Sinclair et al., 2003). These suggestions are, however, also difficult to reconcile with the cut-mark distribution data discussed above, since the same elements of size 3 bovids with abundant cut-marks at FLK-Zinj tend to be defleshed quickly by lions (O’Connell et al., 1988b; Domínguez-

Rodrigo, 1999; Bunn and Pickering, 2010; Gidna et al., 2014). Furthermore, the mortality profiles of lion kills are significantly different to that seen at FLK-Zinj, and the penecontemporaneous site of DS, as the former tend to include substantially fewer prime adults (Bunn and Pickering, 2010; Bunn and Gurtoy, 2014; Cobo-Sánchez, 2020). Lastly, studies on the behavioral ecology of carnivore predation have shown that extant lions tend to preferentially target larger prey sizes when they are available, especially buffalo (size 4), across a range of ecosystems (Funston and Mills, 2006; Davidson et al., 2013; Dublin and Ogutu, 2015). This contrasts with the predominance of size 1–3b bovids in anthropogenic Olduvai Bed I assemblages (Bunn and Pickering, 2010; Cobo-Sánchez, 2020), further emphasizing that large felids were unlikely to have been the main agent of accumulation at FLK-Zinj.

At FLK-Zinj, there is a single high-density cluster of faunal remains (Leakey, 1971). While bone refuse in modern hunter-gatherer campsites tends to display a multi-cluster distribution that differs from the FLK-Zinj pattern (Domínguez-Rodrigo and Cobo-Sánchez, 2017), the high density of remains at the site mirrors the abundance of bone leftovers noted for dry season Kua camps in the Kalahari (Bartram et al., 1991). While ca. 23% of the analyzed assemblage exhibits tooth-marks (Domínguez-Rodrigo et al., 2007; Parkinson, 2018), their distribution is not clustered on primary-access areas, and thus they do not challenge the predominantly anthropogenic origin of the assemblage (Parkinson, 2018). Instead, on the basis of the morphometry of tooth marks on cancellous bone and the deletion of epiphyses, ribs, and pelvis fragments, it appears that hyenids subsequently ravaged the FLK-Zinj faunal assemblage, which would account for the high tooth mark frequencies (Domínguez-Rodrigo and Barba, 2006; Parkinson, 2018). These secondary scavengers were likely attracted to the high concentration of bone refuse, scattering some of the

remains away from the main cluster in the process (cf., Camarós et al., 2013; Domínguez-Rodrigo and Cobo-Sánchez, 2017).

In addition to the zooarcheological and taphonomic data, actualistic insights from bovid ecology can help elucidate further the nature of hominin carcass acquisition at the site. Since *Kobus sigmoidalis* is the most abundant size 3 bovid at FLK-Zinj (Bunn and Pickering, 2010), we center our discussion around it. This extinct waterbuck species is similar in size and phenotype to the extant *Kobus ellipsiprymnus* in East Africa, presumably occupying similar habitats (Spencer, 1997). The species is gregarious and non-migratory (Foley, 1983), living in groups of 6–30 individuals. Waterbuck stay near active water sources, particularly during the dry season, since waterbuck do not tolerate dehydration well (Taylor et al., 1969; Foley, 1983; Estes, 2004).

Females and their offspring form nursery herds, whereas young males unite in bachelor herds, roaming the landscape in pursuit of an opportunity to displace the prime territorial male, which is most dominant at 6–9 years of age (Kingdon and Hoffman, 2013). However, territorial competition between bachelor herds and dominant males often results from the decrease in food availability associated with the dry season (Tomlinson, 1979; Tomlinson, 1981). These tensions lead to increases in activity which, alongside the decrease in food intake, is known to result in a substantial decline in body condition in impala and other antelope species during periods of competition, such as the rut (Murray, 1982; Van Rooyen, 1993). Around the age of ten, the primacy of territorial males is often irrevocably challenged and they are replaced. After losing their status and territory, these late prime males recede to small and unprotected areas of the landscape, which renders them more vulnerable to predators (Kingdon and Hoffman, 2013). These late prime individuals, however, are not yet ontogenetically old, since waterbuck live around 18 years in the wild. As such, dry season hunting strategies should have avoided the acquisition of territorial,

prime-aged males, not only because they might have been more difficult to hunt, but also because they would have experienced fat depletion much quicker than other age and sex groups, such as late prime males and especially pregnant waterbuck females. Kidney fat indices for many species, such as impala (*Aepyceros melampus*) and nyala (*Tragelaphus angasii*), tend to be higher in pregnant than non-pregnant individuals (Spinage, 1984).

A detailed examination of the waterbuck adult sample at FLK-Zinj ($n = 7$) shows that there is a complete absence of peak prime-aged males (Bunn and Pickering, 2010). The sexual dimorphism of this species allows the identification of three smaller, early prime females and four larger, late prime males, which Bunn and Pickering (2010) suggest could represent these older, non-territorial individuals. Furthermore, on the basis of unworn upper and lower deciduous premolars, at least two, likely three, fetal individuals are present in the assemblage, which suggests that the early prime females were captured during late gestation (Bunn and Pickering, 2010). During this stage, pregnant female ungulates are most vulnerable to predation (Molinari-Jobin et al., 2004; Owen-Smith, 2008). Furthermore, adult waterbuck females are observed in open forested environments much more often than expected when compared to territorial and bachelor males (Wirtz and Kaiser, 1988), perhaps making their presence in the woodland surrounding FLK-Zinj more likely. Therefore, while the adult waterbuck individuals were ontogenetically prime, the overrepresentation of pregnant females and late prime males suggests that hominins at FLK-Zinj were more successful when targeting nursery herds and lone individuals as they passed through woodland on approach to the perennial spring. Increases in hunting success rates would have ensured that more individuals within the group obtained access to meat-derived nutrients (Kaplan and Hill, 1985; Speth, 1990; Tennie et al., 2009).

As such, we argue that Oldowan hominins enjoyed higher success rates when engaging in compensatory hunting strategies targeting seasonally-vulnerable prey demographics. The active exploitation of fleshed carcasses during the dry season would have provided hominins with early access to energy-dense resources, such as meat (~15% of bone specimens at FLK-Zinj display cut-marks; Parkinson, 2018) and within-bone nutrients, such as marrow (22–23% exhibit percussion marks; Domínguez-Rodrigo et al., 2007; Parkinson, 2018). The resulting composition of the assemblage, biased towards individuals who would subsequently be more likely to succumb to physiological stress later in the dry season, may also help explain the degree of overlap in mortality profiles between FLK-Zinj and the mostly non-anthropogenic ‘background’ assemblages at other Olduvai Bed I sites (Bunn and Pickering, 2010: Figure 3).

We also suggest that dry season hunting patterns may have played a role in the expedient nature of the lithic toolkit at FLK-Zinj, suggested by the overall predominance of relatively simple unidirectional and unifacial reduction schemes and the lack of retouch on flakes (de la Torre and Mora, 2005; Gallotti, 2018). Our seasonality framework would suggest that the meat and within-bone nutrients of terrestrial ungulates were important resources for hominins throughout most of the dry season, as they are for the Hadza (Bunn et al., 1988; Hawkes et al., 1991; O’Connell et al., 1992; Marlowe and Berbesque, 2009). Future use-wear analysis will help to test this at FLK-Zinj (cf., Bello-Alonso et al., 2019). Nevertheless, successful carcass acquisition endeavors may have been rather unpredictable at the daily scale (Hawkes, 2000), making it more difficult to time the use of tools throughout the landscape. In this context, we note the finding of Binford (1979) that the lithics produced by the Nunamiut for an immediate need were notably less complex than those used in pre-planned activities. Moreover, Kua hunter-gatherer groups in the Kalahari tend to consume carcasses almost immediately during the hot dry season, and transport them only across

short distances, to minimize their exposure to heat and predators (Bartram et al., 1991). Therefore, while short-distance movement of carcasses from acquisition spots to the woodland ecotone at FLK-Zinj provided some relative safety, these hazards would have fostered an expedient toolkit that could be produced quickly to extensively process carcasses in a minimized amount of time.

The butchery activities documented taphonomically at FLK-Zinj heavily emphasize filleting rather than disarticulation (Parkinson, 2018), and slicing meat offers little resistance to lithics (Bello-Alonso et al., 2019). As such, the task can be achieved as successfully with unretouched than with retouched flakes (Jones, 1994), thus discouraging the additional investment required by the latter. That lithics and faunal remains at FLK-Zinj are functionally associated is further supported by their correlated spatial distributions (Domínguez-Rodrigo and Cobo-Sánchez, 2017). Risk-buffering processes may also explain investment in directional quartzite transport into the site from the Naibor Soit, rather than use of the local lava cobbles which predominate in Leakey's (1971) unmodified manuports (de la Torre and Mora, 2005). Quartzite flakes display greater initial edge sharpness despite their reduced durability, and thus its selection suggests a desire to maximize efficiency in short-term tasks (Key et al., 2020). In this context it is interesting to note that such a preference for quartzite over basalt flakes (and handaxes) is directly associated with butchery practices at the Bed II sites of FLK-W and BK (Yravedra et al., 2017a; Yravedra et al., 2017b). Hominins were thus likely to have been planning their repeated visits to the site following acquisition of carcasses during the dry season (Domínguez-Rodrigo et al., 2010). This behavioral scheduling would have provided an opportunity to minimize the costs of transporting quartzite across the landscape during hunting forays by maintaining a raw material presence at a known processing spot, and quickly producing usable flakes when carcasses were brought to the site (cf., Potts, 1984; Potts, 1991).

5. Discussion

5.1. Seasonality and Oldowan behavioral flexibility at Kanjera South and FLK-Zinj

As outlined above, we argue that the available data from Kanjera South (Kenya) and FLK-Zinj (Olduvai Gorge, Tanzania) evidence a pattern of seasonal variation in Oldowan subsistence strategies, which underscores the behavioral flexibility of early *Homo*. The term ‘behavioral flexibility’ has a long history of use in relation to animal learning and adaptation in the fields of behavioral psychology and behavioral ecology (e.g., Dickinson, 1981; Kummer and Goodall, 1985; Tebbich et al., 2010; Navarrete et al., 2016; Audet and Lefebvre, 2017). The term is used here simply to highlight the problem-solving skills of Oldowan hominins, for whom seasonal shifts would have constantly re-structured acquisition priorities on the basis of resource quality and availability.

Using the nature of resource acquisition and processing at FLK-Zinj and Kanjera South as a lens to study these phenomena, we suggest that seasonality played a profound role in the subsistence strategies of Oldowan hominins, mirroring observations made in extant nonhuman primates and modern human hunter-gatherers. Regarding terrestrial animal consumption specifically, compensatory hunting strategies targeting vulnerable prey demographics emerged at both sites, but differ in ways consistent with predictable seasonal cycles. At Kanjera South, small bovid hunting focused on the exploitation of young individuals (Ferraro et al., 2013), perhaps through the location and pursuit of newborn calves in the longer grasses (Oliver et al., 2019). On the basis of small savanna bovid ecology, we argue that such a hunting strategy is more likely to have been undertaken during the wet season, since most births tend to take place around the onset of the rains (Sinclair et al., 2000; Kingdon, 2015; Pobiner, 2020). As such, this strategy would not

have been as readily available at FLK-Zinj during the dry season. Instead, these hominins predominantly targeted the vulnerability of pregnant or older individuals.

Meanwhile, carcass processing at Kanjera South was generally less intensive than at FLK-Zinj, both in terms of defleshing and limb bone marrow processing (Domínguez-Rodrigo et al., 2007; Ferraro et al., 2013; Parkinson, 2013; Parkinson, 2018). Instead, hominins at Kanjera South preferentially targeted the brains and/or cranial pulp of large bovid skulls as well as mandibular nerve and marrow (Ferraro et al., 2013), resources that would have maintained a greater fat content into the early wet season (Sinclair, 1975). In this context, we suggest that activities enabling access to consistently fat-rich resources, such as evisceration and brain extraction, would have been particularly important during these periods of ungulate depletion. In contrast, the utility of defleshing and marrow extraction would have been much greater when bovid fat stores were more substantial. We also speculate that disarticulation may have been more relevant throughout the wet season as a whole, as ungulate dispersal and hominin movement through the landscape were generally more extensive. Nonetheless, we note that ethnoarcheological assessments of differential body part transport by animal condition (pregnant, juvenile, feeble) or season of acquisition are limited by small sample sizes (Lupo, 2006), meriting further research.

As ungulate carcasses exhibit fat depletion from the very late dry season into the wet season (Sinclair, 1975; McNaughton and Georgiadis, 1986), a contextual paleoecological assessment (Table 5) can assist in discerning seasonality when taphonomic research indicates a degree of meat and marrow avoidance (Speth, 1987; Blumenschine and Marean, 1993; Bunn and Ezzo, 1993). For example, within the Lower Augitic Sandstone (LAS) unit of HWK-EE (Olduvai Gorge), Pante et al. (2018) report a pattern of fat-depleted marrow and epiphyseal grease avoidance by both carnivores and hominins, characterized by high epiphyseal to shaft fragment ratios (0.23; cf.,

Blumenschine and Marean, 1993) alongside low tooth mark (5.4%) and percussion mark values (7.8%). The proportion of midshaft fragments with percussion marks closely mirrors the 6–9% values reported for Kanjera South and are well below those from FLK-Zinj (Ferraro et al., 2013; Parkinson, 2018). This relatively limited engagement with within-bone nutrients occurs alongside cut-marked hippopotamid remains, a considerable number of shed crocodile teeth (Pante et al., 2018), and a notable concentration of fish remains suggesting a catastrophic mortality episode (Bibi et al., 2018). This mortality profile is expected from modern observations of fish becoming trapped in pools as the water recedes in the late dry season (Leakey, 1971; Stewart, 1994). Extant crocodiles also tend to congregate within increasingly isolated pools of water towards the end of the dry season (Njau, 2012), a time they are known to share them with hippopotami (Kofron, 1993). This suggests an occupation of LAS at HWK-EE that encompassed the very late dry season, which would be consistent with the more general dry season indication given by bovid tooth micro- and meso-wear data (Rivals et al., 2018).

Given the patterns of marrow and grease avoidance, it is perhaps surprising that pounding and/or percussive tools at HWK-EE (found in greater number than at any other Olduvai Bed I–II site) are most abundant within the LAS ($n=283$; 81.1%; Arroyo and de la Torre, 2018). The intensity of contact on the active areas of most of these tools suggest a direct percussive motion and use in hard hammer lithic manufacture (Arroyo and de la Torre, 2016, 2018). Many hammerstones with active edges (HAE), anvils, and subspheroids, however, have lower-intensity wear patterns (Arroyo et al., 2018). Experimental tools used to open nuts, tenderize meat, extract marrow from limb bones, and process tubers show low-intensity wear (de la Torre et al., 2013; Sánchez-Yustos et al., 2015; Arroyo et al., 2016). In this regard, the limited evidence for percussive breakage of bone shafts in this late dry season context (Pante et al., 2018) may suggest that these

pounding tools may have targeted resources other than marrow. In particular, nuts and seeds can represent an attractive seasonal source of unsaturated fats, often linked with the ripening (and rotting) of fruits and grasses at seasonal transitions (Testart, 1982; Hitchcock et al., 1996; Eaton et al., 1997; Lee 2013; Lombard and Kyriacou 2018). Procurement and consumption of nuts throughout the dry season is amply documented among African hunter-gatherers in both tropical rainforests and more open environments (Kitanishi 1994; Hitchcock et al., 1996; Sato et al., 2012; Lee, 2013; Remis and Jost Robinson 2014; Gómez et al., 2016; Ingram et al., 2017). Nuts and seeds may therefore have been possible resources requiring pounding that could compensate for fat depletion in Oldowan food procurement strategies, particularly during the very late dry season.

Table 5: Summary of predictions discussed in the text for assessing seasonality of site use in the Oldowan, derived from the comparison of Kanjera South and FLK-Zinj and incorporating insights from other Early Pleistocene localities discussed in the text. Presence or absence of migratory taxa may also be a relevant seasonal, landscape-specific paleoecological signature. Note that hominin occupation at some Oldowan sites may span more than one season or a seasonal transition (potentially including FwJj20), while natural site formation processes may also result in the deposition of background material from successive seasons. With regards to assessments of mortality profiles, skeletal part profiles, and spatial distribution of faunal remains, it is important to consider the impact of secondary carnivore ravaging, post-depositional transport, and bone preservation biases due to biogeochemical processes. Any of these factors would compromise the integrity of the faunal assemblage, making inferences regarding the specific nature and intra-annual timing of hominin activity more difficult.

973	Season	Paleoecological signatures	Taphonomic patterns	Habitat selection	Lithic evidence
Dry season	Broadly dry season	Clustering of water-dependent taxa Higher carnivore competition	Greater emphasis on defleshing High-density, clustered distribution of faunal remains	Perennial springs and watercourses Mosaic woodlands offering tree cover	Shorter transport distances More expedient reduction schemes Limited emphasis on flake retouch Greater use-wear emphasis on animal butchery
	Very late dry season	Shed crocodile teeth Mass fish concentrations High co-occurrence of crocodile and hippopotamus remains	Marrow and meat avoidance		
Wet season	Broadly wet season	High plant biomass availability Lower carnivore competition Abundance of testudine remains	Greater emphasis on evisceration Lower densities of faunal remains	Fluvial contexts and seasonal watercourses Grasslands	Increased transport distances More intensive reduction schemes Greater emphasis on flake retouch Greater use-wear emphasis on plant processing
	Early wet season	Abundance of bovid juveniles Catfish in fluvial contexts	Emphasis on head contents Limited emphasis on meat and marrow		

In contrast to HWK-EE, we would suggest that palaeoecological indicators suggest that the bulk of hominin activity at Kanjera South likely occurred in the wet season. The opportunistic availability of medium-large bovid heads from carrion pulses and/or carnivore kills may mean that occupation of the site began in the very late dry, but only the early wet would account for the abundance of juvenile bovids in the context of the renewal of plant biomass in this grassland ecosystem. Furthermore, the aforementioned rarity of water-dependent reduncines at Kanjera South stands in contrast to the predominance of *Kobus* at FLK-Zinj (Oliver et al., 2019), despite both sites having a perennial water source nearby. Waterbuck are known to show a tight relationship between habitat quality and population density, with feeding areas clustering around water sources in the dry season and dispersing into well-watered open grasslands with the onset of the rains (Tomlinson, 1981; Spinage, 1982; Wirtz and Kaiser, 1988). Therefore, the contrasting patterns of reduncine abundance at FLK-Zinj and Kanjera South are consistent with a broadly wet season attribution to the latter.

The prevailing character of the FLK-Zinj lithic assemblage is one of expediency, as indicated by the predominance of unifacial, unidirectional reduction strategies, and only very limited secondary retouch (Leakey, 1971; de la Torre and Mora, 2005; Gallotti, 2018). Some of this reduced investment may be related to the relatively reduced cost of abandoning a local raw material, and indeed different Oldowan sites at Olduvai show a linear reduction in the weight, density, proportion, and reduction intensity of quartzite raw material in the assemblage with distance from the Naibor Soit (Blumenschine et al., 2008). However, there are clear deviations from this trend which may suggest additional ecological influences on the lithic assemblages, with Blumenschine and colleagues (2008) suggesting that the magnitude of the deviations from the distance-decay trend may be related to the extent of task-specific raw material utility

(Blumenschine et al., 2008). Indeed, the functional expediency at FLK-Zinj is underlined by the likely selection of quartzite materials (over the more durable and immediately local lava) for their cutting efficiency (Key et al., 2020).

This contrasts with the pattern at Kanjera South, where selection of materials emphasized durability over flaking predictability (Braun et al., 2009a). Had Kanjera South shared a similar emphasis on the fast production and use of raw material with FLK-Zinj, we would have expected flaking predictability to have been a more important factor in the knapping of material. Instead, the hominins at the site were willing to accept a greater risk of shorter flakes with less sharp edges and a greater chance of hinge and step fractures in order to produce more durable cutting edges (Braun et al., 2009a). This emphasis on tool durability at Kanjera occurs alongside the aforementioned increased frequency of investment in reduction (particularly bifacial centripetal reduction schemes), producing longer cutting edges relative to flake mass, and in secondary retouch, with certain raw materials being transported into the site from >10 km away (Braun et al., 2008; Braun et al., 2009a; Braun et al., 2009b; Reeves et al., 2021). This implies a decoupling of lithic use from specific points on the landscape (cf., Braun and Harris, 2003). In addition, non-local materials at Kanjera tend to be among the most durable, and show the most retouch (Braun et al., 2009a; Braun et al., 2009b; Lemorini et al., 2014), a technological strategy that would have enhanced further the potential use-life of the tools (Jones, 1981). This trade-off implies that hominins were planning more abrasive or time-consuming activities such as skinning and/or the processing of medium-hard plant tissues (Braun et al., 2009a). Indeed, use-wear evidence at Kanjera South confirms that a substantial quantity of lithic implements were primarily devoted to the processing of plant resources (Lemorini et al., 2014; Lemorini et al., 2019). Recent experimental studies have shown that flake retouch and larger flake sizes, which increase force

loading and manipulability, enhance wood processing efficiency, suggesting that plant resource manipulation directly influences lithic investment (Bencomo Viala et al., 2020; Gürbüz and Lycett, 2021). These patterns may reflect the establishment of a processing chain to enhance resource procurement through organic tool use (cf., Pascual-Garrido and Almeida-Warren, 2021).

We use these observations as an empirical basis from which to develop predictions regarding the relationship between seasonality and technological investment in the Oldowan. According to evolutionary optimality theory, organisms attempt to maximize a particular currency variable, such as nutrient return rates, with decisions made according to the costs and benefits of a particular action, in the context of available constraints (Hawkes et al., 1982; Foley 1985; Stephens and Krebs, 1986; Winterhalder and Smith, 1992; Ferraro, 2007; Kelly, 2013). In this context, we emphasize the relevance of seasonal variables, such as competition risk, resource type and quality, acquisition costs, and resource predictability, for understanding the level of expected technological investment in lithic assemblages. In Figure 2, these seasonal variables can be considered intra-annual constraints on technological development, informing the relative costs (processing requirements) and benefits (expected returns) on such investment.

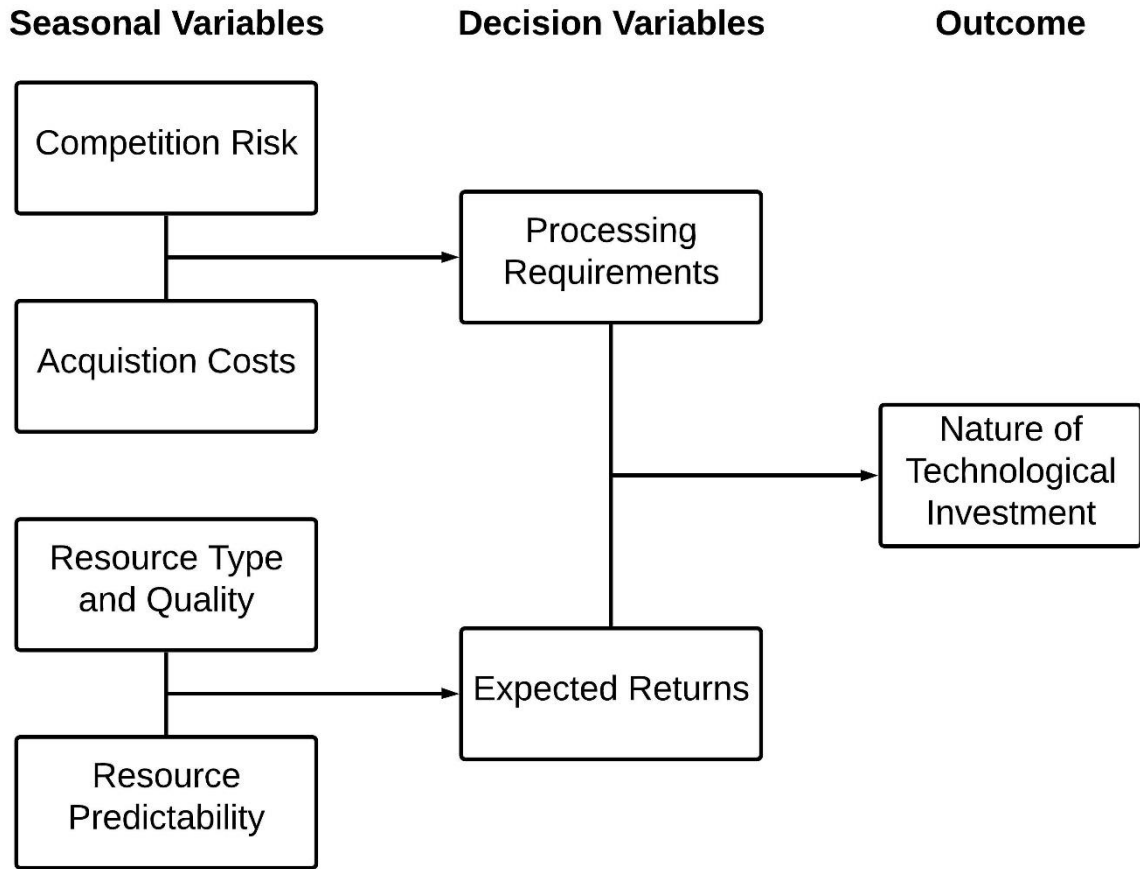


Figure 2. Expected relationship between resource seasonal resource procurement and technological outcomes in the context of Oldowan.

Faunal acquisition during the Oldowan relied on the relatively unpredictable exploitation of sparse and mobile resource patches, at least partially through compensatory hunting at both Kanjera and FLK-Zinj. The use of such hunting strategies is likely to have reduced the unpredictability of return yields associated with other carcass acquisition strategies, but it still would not have approached the predictability of distribution and returns seen in plant resources, particularly during the wet season. Indeed, modern observations of the Hadza suggest men only succeed in obtaining large carcasses in 1 in 30 hunter-days, remaining as low as 1 in 3 when small game hunting and trapping was carried out (Hawkes et al., 1991; Hawkes et al., 2001). Given that Oldowan hominins lacked the technological complexity observed in the Hadza, particularly bows

and arrows, we can envisage even greater failure rates in the Early Pleistocene. Furthermore, experimental studies have suggested that retouched flakes are not more effective in this task than unretouched flakes (Jones, 1994), suggesting that increased investment for predominantly defleshing purposes will not always produce a corresponding dietary return. In this context, returns on investment towards carcass processing beyond expedient unretouched flakes upon procurement would have been minimal relative to costs and relatively unpredictable. Furthermore, the spatiotemporal co-occurrence of hominins and carnivores in the ecosystem during the dry season demanded the evaluation of trade-offs between defending or abandoning a carcass before complete exploitation. Time constraints associated with predation risk have been suggested to directly influence lithic reduction sequences and Oldowan tool use at Swartkrans, South Africa (Caruana, 2020). Taken together, we would expect a greater emphasis instead on an expedient flake toolkit capable of fast carcass processing in dry season contexts, as observed at FLK-Zinj.

In contrast, investment in increased handling efficiency is most effective when search costs are minimal in relation to time spent harvesting and processing a resource (Hawkes and O'Connell, 1992; Hawkes et al., 2018). In the context of increased plant availability and diversity in the wet season (Sept, 1984), knowledge regarding the abundance and predictability of visible and embedded resource distributions may have minimized search times and reduced resource procurement competition (cf., Foley, 1985; Clark and Linares-Matás, 2020). In addition, given the greater energy density of animal resources (particularly fat: 9 kcal/gram), plant carbohydrates will generally produce lower caloric return per unit of weight (4 kcal/gram) and unit of handling time (US National Research Council on Diet and Health, 1989; Stewart, 2014). This further elongates the required amount of time spent handling these resources to meet caloric requirements (Hawkes et al., 1982). These factors would have fostered investment towards minimizing handling costs

and maximizing overall return rates, while also allowing for the ability to foreplan the use of lithic technology throughout the landscape (Clark and Linares-Matás, 2020). Taken together, we would therefore expect greater investment in raw material selection and transport (where high-quality local materials are not available) at wet season sites. This should result in a corresponding increase in lithic reduction intensity and in the diversity of final forms, including an extent of secondary retouch. We argue that these patterns are reflected in the relative lithic complexity observed at Kanjera South (Braun et al., 2009b; Lemorini et al., 2014; Reeves et al., 2021).

5.2. Seasonality and habitat selection in the Oldowan

A recent comparison of faunal exploitation between Kanjera South and FLK-Zinj emphasized that the affordances of different habitat types, such as grasslands and woodlands, heavily influenced specific modes of hominin resource acquisition (Oliver et al., 2019). While this is certainly true, seasonal constraints and opportunities would have actively influenced Oldowan habitat selection patterns. Predictable response patterns to seasonality-mediated changes in habitat composition, suitability, and the spatial distribution of preferred resources have been documented for a wide range of genera across a diversity of heterogeneous ecosystems (e.g., Fleming et al., 1987; Van Schaik et al., 1993; Pape and Löffler, 2015; Vélez et al., 2017; Stanley et al., 2021), including chimpanzees in forest-woodland mosaic environments (Collins and McGrew, 1988; Pennec et al., 2020). Moreover, modern human hunter-gatherers show clear patterns of seasonal movement, with camps tending to be located near perennial water sources during the (late) dry season (e.g., Hawkes et al., 1997; Lee, 2013). Among the Hadza, wet season camps are more ephemeral, with repeated camp movement determined by relatively frequent fluctuations in the spatio-temporal distribution of berries and honey (Hawkes et al., 1997).

We argue that predictable fluctuations in the spatio-temporal distribution of resources would have encouraged Oldowan groups to schedule their food-procurement strategies, technological investment, and preferred habitats on the basis of seasonal constraints and opportunities. The lakeshore grassland environment at Kanjera South would have enjoyed moist soils and ephemeral watercourses during the wet season (Ditchfield et al., 2019), which would have profound implications for plant resource availability and seasonal habitat attractiveness for Oldowan hominins and other animals. In the context of modern hunter-gatherer seasonal foraging strategies, the Hadza specifically target environments rich in berries, such as the floodplain of the Barai River near Lake Eyasi (Vincent, 1985), with the availability of these berries even dictating the location of many wet season camps (Hawkes et al., 1997). We also note that the probability of finding medium- to large-sized carcasses with scavenging potential during the wet season in the Serengeti increases along erosion embankments and the margins of riparian woodlands (Blumenschine, 1987; Hopcraft et al., 2005). In contrast, the mosaic woodland with perennial springs around FLK-Zinj (Ashley et al., 2010) would have been an attractive dry season hotspot for ungulates, carnivores, and hominins seeking water and other resources (Hopcraft et al., 2005; Hawkes, 2016).

We also emphasize that our proposed model regarding the nature of lithic investment at Oldowan sites may be reinforced by raw material management strategies in relation to the length of site occupation in the face of seasonal variability in habitat selection. In the context of the Late Pleistocene, Riel-Salvatore and Barton (2004) point out that longer-term occupation of a site, especially where raw material has been cached, should be associated with reduced intensity of reduction and curation, as the pressure on preserving raw material is lower. In turn, this should result in greater artifact densities at such a site, but with an overwhelming focus on unretouched flakes. Thus, site-level raw material provisioning in the context of a longer duration of

occupation(s) near perennial water sources during the dry season may have contributed to the patterns observed at FLK-Zinj. In contrast, in contexts of higher mobility across the landscape and shorter occupations, hominins should be faced with greater constraints on raw material availability, resulting in a need to more efficiently utilize (transported) raw material through intensive core reduction and flake maintenance through edge retouch. This may relate to the technological patterns observed at Kanjera South (Reeves et al., 2021), in the context of wet season foraging activities.

5.3. Seasonality and freshwater resource exploitation in the Oldowan

Terrestrial animal and plant resources were certainly not the only components of Oldowan diets. In particular, freshwater resources such as crocodiles, testudines, fish, or shellfish would have offered rich polyunsaturated and Omega-3 fatty acids, as well as trace minerals and vitamins (Stewart, 1994; Braun et al., 2010; Archer et al., 2014; Cáceres et al., 2017). These resources exhibit relatively predictable distribution patterns and availability peaks, being most easily captured during the very late dry and early wet seasons (Stewart, 1994), the periods when terrestrial animal resources would have been most fat-depleted. Furthermore, the intra-annual patterns of behavior in many freshwater taxa can act as important paleoecological information for inferring the seasonality of site formation.

At Olduvai, the fish assemblages ($n = 4000$) of Bed I and II sites exhibit low taxonomic diversity, likely due to the high salinity and alkalinity values of the Olduvai paleolake (Greenwood and Todd, 1970; Stewart, 1994). At FLK-Zinj, the assemblage (number of identified specimens [NISP] = 110) comprises predominantly catfish (83.3%) and cichlids (16.7%; Stewart, 1994). While most Olduvai Bed I fish assemblages are likely the result of natural depositional processes,

1139 FLK-Zinj and FLK-NN have a relatively greater density than natural lacustrine fish scatters, and
1140 an overrepresentation of head versus axial fragments, which may indicate that hominins were
1141 acquiring and processing them (cf., Stewart, 1994). Nonetheless, since the fish assemblage at FLK-
1142 Zinj represents a small proportion of the overall faunal assemblage, fish procurement may have
1143 been opportunistic (Stewart, 1994), perhaps based on the capture of stranded specimens as the
1144 paleolake and seasonal watercourses to the south of the site (Uribelarrea et al., 2014) were receding
1145 during the dry season. Catfish and cichlids are also present within the Kanjera South fish
1146 assemblage (Plummer et al., 1999; Archer et al., 2014), but they do not bear diagnostic surface
1147 modification damage (J. Ferraro, pers. comm.).

1148 A key site for understanding the combined freshwater and terrestrial resource exploitation in
1149 the Oldowan is FwJj20, Koobi Fora Formation, Kenya (1.95 Ma; Braun et al., 2010; Archer et al.,
1150 2014; see Figure 1 above), located within the fluctuating Il Dura fluvio-lacustrine system (Gathogo
1151 and Brown, 2006). Water-dependent species, such as reduncines, tragelaphines, hippopotamids,
1152 and rhinocerotids dominate the terrestrial assemblage, while the sizeable freshwater assemblage
1153 includes turtle, fish, and crocodiles (Braun et al., 2010; Archer et al., 2014). Taphonomic evidence
1154 indicates primary hominin access to the carcasses, with cut-mark distribution data indicating the
1155 practice of evisceration, disarticulation, and defleshing (Braun et al., 2010). Viscera extraction on
1156 terrestrial carcasses is inferred on the basis of cut-marks on the ventral side of a rhinoceros rib (cf.,
1157 Nilssen, 2000), and disarticulation is evident from the presence of cut-marks on a hippopotamus
1158 astragalus and on the glenoid fossa of a bovid scapula (Braun et al., 2010). Flesh removal was
1159 documented on the palmar surface of a crocodile phalanx, which Braun et al. (2010) suggest would
1160 have granted hominins access to the manus muscle mass. The abundance of plastron and carapace
1161 elements indicates that the chelonian assemblage at FwJj20 is anthropogenic in nature (cf.,

Sampson, 2000), while the presence of cut-marks on the ventral surface of a turtle costal carapace element indicates that evisceration was also being carried out on turtle carcasses (cf., Blasco, 2008; Braun et al., 2010). With regards to fish, the FwJj20 assemblage (NISP = 405) is dominated by catfish (NISP = 365, MNI = 49). The catfish skeletal part profiles show an over-representation of cranial fragments (ca. 75%; Stewart, 1994; Braun et al., 2010; Archer et al., 2014). Archer et al. (2014) notes that head over-representation is often the result of butchery processes, as further evidenced by the presence of cut-marks (mostly on cranial fragments), as well as intentional fragmentation. 25.5% of cranial fragments have green breakage planes—with 27.5% of these initiated along sutures—and 2.5% exhibit percussion marks and associated notches (Archer et al., 2014). On the basis of catfish butchery experiments engaging local Turkana fishing communities, cranial breakage along sutures using a hammerstone appears to be strongly associated with access to the fat-rich brain matter (Archer et al., 2014).

Archer et al. (2014) suggest that the main drivers of hominin exploitation of freshwater resources may have been attempts to reduce energetic investment in resource acquisition, to reduce technological costs, or to reduce carnivore competition. Additionally, their exploitation may have been related to seasonal periods of animal depletion and diminishing body fat percentages (Archer et al., 2014). Carnivore tooth mark patterns on limb bone fragments at FwJj20 (1.9% NISP) indicates that carnivore competition in this riparian woodland setting (Bamford, 2011) was lower than at both the dry season mosaic woodland environment at FLK-Zinj or the wet season open grassland environment at Kanjera South. As such, rather than representing primarily an attempt to avoid carnivore competition, we concur that low procurement costs may have facilitated the seasonal exploitation of fat-rich freshwater resources by hominins. Hominins at FwJj20 appear to have exploited terrestrial animal resources rather selectively, given the evidence for evisceration

and skeletal part selection through disarticulation alongside comparatively little evidence for terrestrial carcass filleting at the site (Braun et al., 2010). Similarly, percussion marks on terrestrial limb bones are low ($n = 4$), suggesting little emphasis on limb bone marrow nutrients of terrestrial animals (Braun et al., 2010: Table 2), confirming the overall signature of less intensive carcass processing than at FLK-Zinj. These taphonomic insights are consistent with a pattern of seasonal fat-depletion in the flesh and marrow of African ungulates (cf., Sinclair, 1975; Speth, 1987).

On the basis of fish ecology, the reliance on catfish exploitation within a humid fluvio-lacustrine context at FwJj20 may also be used to infer seasonality of occupation, as the aforementioned catfish engage in mass riverine migration towards the onset of the early rainy season to spawn (Stewart, 1994). Intensive catfish exploitation in a fluvial context has also been reported at BK in Olduvai Bed II, and was used by Stewart (1994) to infer a very late dry to early wet season context, potentially allowing the same deduction to be applied to FwJj20. A hominin presence spanning this seasonal transition would also be consistent with the diverse paleoecological signatures observed at the site. For example, the high density of water-dependent reduncine remains and the co-occurrence of abundant crocodile and hippopotamid remains would indicate late dry season, while the high proportion of chelonid, in relation to bovid NISP values would be suggestive of wet season (cf., Speth and Davis, 1976). Embedded fish resources, such as the energy-dense head content of catfish, appear to have been particularly desirable to the FwJj20 hominins (Archer et al., 2014). Since catfish brains have a similar metabolic composition to mammalian brains (Du et al., 2018), they likely performed a similar dietary function at FwJj20 to the large bovid heads and mandibles processed at Kanjera South (Ferraro et al., 2013) in the seasonal food-procurement schedules of early *Homo*. It is also possible that the cut-marks found on a crocodile skull fragment at Gona OGS-6 (Cáceres et al., 2017) may have similarly been

produced during butchery processes that targeted within-head contents, in addition to adhering flesh. We anticipate that further publications on the technological sequences and use-wear of the lithics of FwJj20 will allow for more holistic comparisons with other Oldowan sites.

6. Conclusions

In this paper, we have attempted to derive a framework for interpreting the influence of seasonality on hominin behavior within the Oldowan record, using patterns of resource consumption and lithic investment at FLK-Zinj and Kanjera South as a lens through which behavioral variability can be studied. On the basis of zooarcheological assessments of mortality profiles and the taphonomic evidence for early hominin access to carcasses, we argue that at least some extent of compensatory hunting is a shared feature of both sites. Nonetheless, there are differences in prey demographics that can be related to seasonal cycles of vulnerability, matching expectations derived from actualistic observations of carnivore feeding behavior (Owen-Smith, 2008; Pereira et al., 2014; Arriaza et al., 2015). The ability to achieve primary access to terrestrial ungulates in different seasons may be indicative of novel foraging behaviors that enhanced overall resource yields from patchy resources. Late Oldowan hominins may have relied on social networks to identify and pursue carcass acquisition opportunities, while keeping predators away in the process. At the same time, we emphasize that the relative relevance of certain animal resources in Oldowan diets was a distinctly seasonal phenomenon. For example, fat-depleted meat would have been less attractive during periods of nutritional stress (cf., Speth, 1987), such as the very late dry season and the early wet season. In these contexts, energy-dense resources such as ungulate head contents, plant carbohydrates, nuts, and freshwater taxa would have been particularly desirable.

We further argue that seasonal changes to food-procurement strategies, partially mediated through habitat selection, would have contributed to the patterning of techno-economic behavior. Embedded social landscape knowledge would have been an underlying requirement in hominin awareness of changing resource distribution patterns and the ability to successfully track and exploit those resources (Clark and Linares-Matás, 2020). Animal resource exploitation involving fast and comprehensive carcass processing upon procurement encouraged greater lithic expediency at dry season sites, especially when facilitated by raw material place provisioning, as interpreted for FLK-Zinj. In contrast, the nutritional constraints associated with the consumption of fat-depleted terrestrial animal resources during the very late dry season and the early wet season actively encouraged hominins to engage in the preferential selection of fat-rich skeletal parts, such as head contents, mandibular nerve and marrow, and viscerae. Freshwater aquatic resources would have also provided a source of fatty acids at this time of the year, as discussed in relation to FwJj20. The availability, predictability, and dietary relevance of plant resources during the early-mid wet season would have encouraged hominins to shift their overall dietary emphasis towards carbohydrate-rich plants. In this context, planning of subsistence behaviors through the landscape and investment in raw material transport and/or lithic reduction schemes may have allowed for reduced resource acquisition and processing costs, either directly or for the production of suitable tools on organic materials. We propose that these seasonal dynamics could help explain the archeological record of Kanjera South. We suggest that the consolidation and subsequent elaboration of these behavioral patterns allowed early *Homo* to more successfully negotiate seasonal variability in resource predictability and habitat structure from the Early Pleistocene onwards.

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