

1 **Seasonality and Oldowan behavioral variability in East Africa**

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9 **Abstract**

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

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

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

34 **1. Introduction**

35 The Oldowan represents the first geographically and temporally widespread lithic tradition
36 of the African Early Stone Age, and can be characterized by the removal of sharp (often short and
37 thick) flakes from cores by direct percussion, with little secondary modification (Gallotti, 2018;
38 Shea, 2020). Assemblages of this nature first appear around the beginning of the Early Pleistocene
39 (~2.6–2.5 Ma) at Ledi-Geraru and Gona, Ethiopia (Semaw et al., 1997; Semaw et al., 2003; Braun
40 et al., 2019). Their appearance is correlated with a period of major climatic change in East Africa
41 (Plummer, 2004), as the gradual onset of the Northern Hemisphere Glaciation, particularly around
42 ~3.0–2.6 Ma, resulted in demonstrably cooler and more variable worldwide climates (e.g., Lisiecki
43 and Raymo 2005; Herbert et al., 2010; Joordens et al., 2019; Trauth et al. 2021). In Africa, this
44 process may have involved an expansion of grasslands and turnovers in mammalian faunas (e.g.,
45 Vrba, 1985; deMenocal, 1995; Bobe and Behrensmeyer, 2004; deMenocal, 2004; Cerling et al.,
46 2011; Potts, 2012; Potts and Faith, 2015), but these are likely to have been gradual and regionally-
47 distinct (Trauth et al., 2021). An important consequence of these changes is the evidence for an
48 intensification of yearly seasonality to levels comparable to the modern-day by at least 2 Ma
49 (Blumenthal et al., 2019).

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

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

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

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

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

93 Since certain primate genera are known to sporadically consume animal resources (Stanford,
94 2001; Surbeck and Hohmann, 2008; Watts, 2020), occasional omnivory was likely a basal hominin
95 trait (Stanford, 2012; Wood and Gilby, 2017). Nonetheless, meat is still a relatively marginal
96 dietary component in bonobos (*Pan paniscus*; Oelze et al., 2011), while chimpanzees only rarely
97 approach even the lowest levels of meat consumption seen in tropical hunter-gatherer societies
98 (Watts, 2020). Therefore, it is likely that several shifts towards greater emphasis on animal
99 consumption took place during the course of hominin evolution (Speth, 1989; Foley, 2001; Bunn,
100 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; Blumenschine 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.

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

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

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

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

151 Freshwater fish represent one such seasonally-constrained but nutritious food source that
152 carnivores and non-human primates occasionally exploit (Turnbull-Kemp, 1967; Goodall, 1971;
153 Ewer, 1973; Kruuk, 1976; Hamilton and Tilson, 1985; Russon et al., 2014). Freshwater resources
154 are often an important source of essential polyunsaturated fatty acids and proteins for tropical and
155 subtropical hunter-gatherers, potentially playing an important role in human evolution (Broadhurst
156 et al., 2002; Jerardino and Marean, 2010; Joordens et al., 2014; Kyriacou et al., 2016).
157 Consumption of such resources may have emerged in the context of seasonal exploitation of USOs,
158 sedges, seedless vascular plants, and aquatic macrophytes in mosaic riparian environments (Sept,
159 1984; Wrangham et al., 2009; Stewart, 2010; Magill et al., 2016). For example, aquatic USOs
160 (which are not subject to the same soil hardness constraints as terrestrial USOs) are exploited by
161 yellow baboons (*Papio cynocephalus*), to the greatest extent during the dry season, when preferred
162 foods are scarce (Wrangham et al., 2009). The transition between the late dry and early wet seasons
163 is a particularly productive period in these environments for opportunistic human fishing (cf.,
164 Dufour, 1987; Sato et al., 2012). This is underpinned by a requirement for cognitive mapping of
165 seasonal fluctuations in water bodies, and knowledge requirements pertaining to specific seasonal

166 fish behaviors in their habitual watercourses. In Eastern Africa, the late dry season is associated
167 with migratory catfish (*Clarias* spp.) and nesting Cichlidae becoming trapped and exposed in
168 shallow receding ponds (Leakey, 1971). In the early wet season, large quantities of catfish then
169 migrate upriver during the early rains to spawn (Greenwood, 1955), and some perciforms,
170 including cichlids, construct their nests in the shallows of river floodplains and lakes (Stewart,
171 1994). Since cichlids are very territorial, African fisher communities of the Bangwelu Wetlands
172 of northeastern Zambia often make spatial references on their recurrent nesting areas to ensure
173 successful fishing encounters during the wet season (Brelsford, 1946). Thus, fish could have been
174 a seasonally predictable and relatively easy to catch prey for Oldowan groups if they were able to
175 become acquainted with the location and fluctuations of seasonal lakes and streams.

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

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

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

197 In the diets of many modern tropical and subtropical hunter-gatherer populations, animal
198 resources play a relevant role year-round, although meat consumption tends to be most frequent
199 during the dry season. For example, among the Baka, and the Mbuti of the Ituri Forest
200 (northeastern Congo), dry season procurement of mammals is consistently greater than during the
201 wet season (Ichikawa, 1983; Sato et al., 2012). Similarly, the greatest period of meat consumption
202 in the Hadza also occurs in the dry season, reaching ~40% of food brought back to camp by weight
203 in the late dry, and dropping to as little as ~10% during the early wet (Marlowe and Berbesque,
204 2009). Among the Ju/'hoansi, Botswana, this general pattern is replicated, with meat also observed
205 to provide up to 80% of the diet during two months of one particularly severe dry season, when all
206 other resources were rather scarce (Weissner and N!aici, 1998; Lee, 2013). This pattern is likely
207 to result from the interplay between changes to overall resource abundance and to resource quality
208 and ranking by season.

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

212 these animals require access to forage persisting around these areas as well as drinking water to
213 compensate for the dehydration of plant foods (Thrash et al., 1995; Redfern et al., 2003; Chamaille-
214 Jammes et al., 2008; Valeix 2011). This spatial clustering of hunting and scavenging opportunities
215 ensures that predators do not need to spend as much time searching for prey in the dry season, and
216 have a greater success rate in locating them (Bunn et al., 1988; Hurtado and Hill, 1990; Foley,
217 1993; O’Connell et al., 2002; Hawkes, 2016). These animal resources also have a greater dietary
218 return than most individual available plants, which further encourages a shift towards their
219 procurement (Pobiner, 2015). This ecological pattern can help explain why most meat tends to be
220 consumed by the Hadza and other subtropical hunter-gatherers during the dry season, providing a
221 greater dietary contribution in the face of seasonal and inter-annual fluctuations in plant resource
222 availability (Vincent, 1985; Bunn et al., 1988; Hitchcock, 1989; Hawkes et al., 1991; O’Connell
223 et al., 1992; Hawkes et al., 1997; Sherry and Marlowe, 2006; Marlowe and Berbesque, 2009; Lee,
224 2013).

225 At the same time, modern human populations have a limit for protein consumption of around
226 30–40% of dietary calories, with consumption above this threshold exceeding the body’s ability
227 to metabolize urea (Cordain et al., 2000). As a result, repeated consumption of lean meat results
228 in a breach of the ‘protein ceiling’—which may lead to protein poisoning—thus placing relatively
229 tight constraints on its consumption and rendering it an ineffective resource under food stress
230 conditions (Binford, 1978; Speth, 1983; Cordain et al., 2000). Indeed, a pattern of fat-depleted
231 animal avoidance is documented among hunters in semi-arid environments, who may even
232 abandon whole carcasses if they are too lean (Tindale, 1972; Hayden, 1981; Speth, 1983). In a
233 similar fashion, contemporary African fishers may throw fat-depleted fish back to the water
234 (Brelsford, 1946; Jubb, 1967).

235 In contexts of marginal nutritional intake, fat and especially carbohydrates, have a protein-
236 sparing effect, as the body is also able to derive energy from these non-protein sources, thus
237 reducing the metabolic demands associated with amino acid catabolism (Munro, 1964; Richardson
238 et al., 1979; Speth and Spielmann, 1983; Bunn and Ezzo, 1993). During periods of fat-depletion
239 in animal carcasses, Cordain et al. (2000) suggest that hunter-gatherers must either show a
240 preferential selection for fatter individuals or carcass portions, hunt larger animals with greater
241 proportions of body fat, or increase their consumption of plant resources, particularly those with
242 high carbohydrate concentrations. A general preferential selection of fatter animals is reported by
243 many different hunter-gatherer groups across different ecosystems (Tomita, 1966; Hart and Hart,
244 1986; O’Dea et al., 1991). In particular, the hunting of different duiker (*Cephalophus* spp.) species
245 predominantly during the dry season by the Mbuti corresponds to the only period of the year when
246 these animals store substantial mesentery fat, as reflected in high kidney fat index (KFI) values
247 (Ichikawa, 1983; Hart and Hart, 1986). Similarly, Lee (2013) reports that the Ju/’hoansi make their
248 first cut of an ungulate carcass along the breastbone, in order to first check the extent of
249 subcutaneous fat, and gain access to the viscera. This preference for fatty body parts is even a
250 common finding among chimpanzees (e.g., Boesch and Boesch, 1989; Pruetz et al., 2015). For
251 example, Gilby and Wawrzyniak (2018) report that chimpanzee consumption of primate prey at
252 Gombe follows a predictable pattern based on immediate returns, in which energy-dense, fat-rich
253 resources, such as viscerae and head-contents, were usually exploited first. This body of evidence
254 strongly suggests that one of the main attractions of animal carcasses for human and non-human
255 primates is fat-rich tissue (Hayden, 1981; Hill et al., 1984; Lee, 2013). Therefore, the interplay
256 between physiological constraints and prey selection strategies makes body fat fluctuation a

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

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

270 This time lag in ungulate physiology therefore has paramount implications for understanding
271 the impact of seasonal food stress on Oldowan animal food procurement strategies, since it implies
272 that the quality of animal resources will have declined less rapidly than that of plant resources in
273 the dry season (Bunn and Ezzo, 1993). As such, we expect hominin consumption of meat resources
274 to be greater during most of the dry season, excluding the very late dry. In the early wet season,
275 ungulate carcasses would still exhibit a high degree of fat-depletion. Moreover, terrestrial
276 ungulates tend to disperse in the face of wider plant biomass availability with the onset of the rains,
277 resulting in lower encounter rates. At this time of the year, hominins should have therefore
278 preferentially targeted carbohydrate-rich resources (berries, honey, and tubers), and energy-dense
279 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.

291 **3. Carcass acquisition strategies by Oldowan hominins**

292 *3.1. Hunting versus scavenging debate*

293 Early paleoanthropological research was quick to take for granted that hunting was a
294 quintessential activity of early *Homo*, driving their socio-economic and technological organization
295 (cf., Lee and DeVore, 1968). Glynn Isaac's (1978; Isaac, 1984) work contributed to the shift of
296 emphasis towards the underlying social organization, structured through cooperation, a gendered
297 division of labor, and the subsequent sharing of food resources at home bases. This period also
298 witnessed the first detailed zooarcheological and taphonomic research on Early Pleistocene faunal
299 remains as sources of evidence (Behrensmeyer, 1978; Bunn et al., 1980; Binford, 1981; Bunn,
300 1981; Potts and Shipman, 1981). When Binford (1985) analyzed skeletal part profiles and
301 superficially assessed the nature of bone surface modifications at FLK-Zinj, he concluded that
302 hominins appeared to have been marginal scavengers of carnivore kills. This interpretation
303 fostered actualistic research assessing whether hominin exploitation of abandoned carnivore kills
304 could have represented a reliable source of nutrients (Blumenschine, 1986; Blumenschine, 1987;
305 Blumenschine, 1988; Domínguez-Rodrigo, 1994; Domínguez-Rodrigo, 1999; Pobiner, 2015).
306 However, subsequent taphonomic and actualistic research amongst modern hunter-gatherers
307 highlighted the relevance of an abundant representation of high-yielding skeletal parts bearing
308 anthropogenic modifications, such as cut-marks and percussion marks, for identifying stone-tool
309 mediated butchery at FLK-Zinj and Koobi Fora sites (e.g., Bunn, 1986; Bunn and Kroll, 1986;
310 Shipman, 1986; Bunn et al., 1988; O'Connell et al., 1988a; O'Connell et al., 1992).

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

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

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

337 Pereira et al., 2014; Mattison et al., 2016). The Hadza provide a hunter-gatherer example of this
338 phenomenon, as individuals are able to respond quickly to scavenging opportunities, including
339 passive scavenging of within-bone nutrients, when they appear at localities where they actively
340 capture ungulate prey (Bunn et al., 1988; O’Connell et al., 1988b; O’Connell et al., 2002; Hawkes,
341 2016). We suggest that Oldowan hominins were also likely to have displayed the flexibility
342 required to switch between different carcass acquisition and processing strategies (Speth, 1983;
343 Bunn and Ezzo, 1993), particularly when facilitated by the deployment of lithic technologies
344 (Foley, 1985; Ferraro, 2007).

345

346 *3.2. Seasonality, prey selection, and carcass acquisition strategies*

347 There are several possible methods of acquiring animal carcasses: scavenging the remains
348 of animals that have died naturally or through predation (passive scavenging), ‘kleptoparasitism’
349 (confrontational/power scavenging) whereby predators are actively chased away from their kills,
350 ‘compensatory/cursorial predation’ of individuals already vulnerable to death due to age or
351 disease, and ‘additive predation’ of healthy individuals (Schaller and Lowther, 1969; Schaller,
352 1972; Pereira et al., 2014). These strategies are summarized in Table 2 (passive scavenging has
353 been divided into facultative scavenging—feeding on earlier predator kills—and scavenging of
354 natural death pulses), alongside their respective ecological patterning and archeological signatures
355 as a framework for evaluating Pleistocene sites. We recognize that these discrete categories
356 actually fall along an overlapping behavioral continuum of carcass acquisition behavior, and
357 therefore hominins are likely to have employed these strategies at different points in time and in
358 varying frequencies, depending on the potential returns, costs, and constraints in a given context.

359 Seasonality has a profound influence on these decision variables, due to changes in factors
360 such as soil condition, maximum daily temperature, cloud cover, precipitation, animal
361 physiological condition, and prey densities. A wide range of carnivores and human-hunter-
362 gatherers adopt compensatory prey selection strategies that are intrinsically linked to these
363 predictable intra-annual changes. For example, lions (*Panthera leo*) of Hwange National Park,
364 Zimbabwe, preferentially target buffalo (*Syncerus caffer*) year-round, but males show an increase
365 in the hunting of vulnerable juveniles when they become more abundant during the wet season
366 (Davidson et al., 2013). Furthermore, lions opportunistically exploited a range of other seasonally-
367 vulnerable animals, including juvenile elephants taken during very late dry season droughts
368 (Davidson et al., 2013). Leopards (*Panthera pardus*) also actively adapt their prey selection
369 strategies to take advantage of birthing seasons and ecosystem changes (Karanth and Sunquist,
370 1995; Yang et al., 2018).

371 Bunn and Ezzo (1993) argued that a flexible adoption of carcass procurement strategies
372 based on intra-annual body condition variability could have provided hominins with a suitable
373 supply of animal resources at different points of the year. Ethnographic accounts of hunting
374 strategies by San groups in the Kalahari demonstrate a pattern of seasonally-vulnerable ungulate
375 prey selection, targeting animals more prone to tiredness on the basis of attributes that fluctuate
376 over different temporal scales such as reproductive status, age, injury, illness, hunger, or thirst. For
377 example, !Xo and G/wi hunters of the Kalahari choose to pursue certain Bovidae, such as steenbok
378 (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and gemsbok (*Oryx gazella*),
379 during the rainy season, when the wet sand forces open their hoofs and stiffens the joints (Schapera,
380 1930; Liebenberg, 2006). In the dry season, Kalahari hunters prefer to track greater kudu
381 (*Tragelaphus strepsiceros*), eland (*Taurotragus oryx*), and red hartebeest (*Alcelaphus caama*)

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

386 The nature and temporality of carcass acquisition strategies determine the specific animal
387 nutrients and skeletal parts available to Oldowan hominins at any given site (Schaller and Lowther,
388 1969; Bunn and Ezzo, 1993). We can predict a focus on high-ranking (and fatty) viscerae whenever
389 hominins had primary access to the carcass (e.g., Lee 2013; Gilby and Wawrzyniak, 2018), most
390 clearly documented through cut-marks on the ventral side of ribs (cf., Nilsson, 2000). This would
391 have been particularly important to hominins during seasonal fat-depletion in terrestrial ungulate
392 carcasses (very late dry to early wet transition), where meat itself becomes very lean. Other
393 elements with high fat availability that are often left by large felids, such as head contents or the
394 marrow of limb bones (Pobiner, 2015), are likely to have been favored whenever available,
395 regardless of the timing of access to the carcass (Thompson et al., 2019). This pattern may have
396 been exacerbated seasonally, with focus shifting towards bones that retain the greatest overall
397 amounts of fat, such as the tibiae, or those which deplete more slowly, such as the lower limb
398 bones (Newlin and McCay, 1948; Turner, 1979; Speth, 1987; Speth, 1990; Blumenschine and
399 Madrigal, 1993).

400

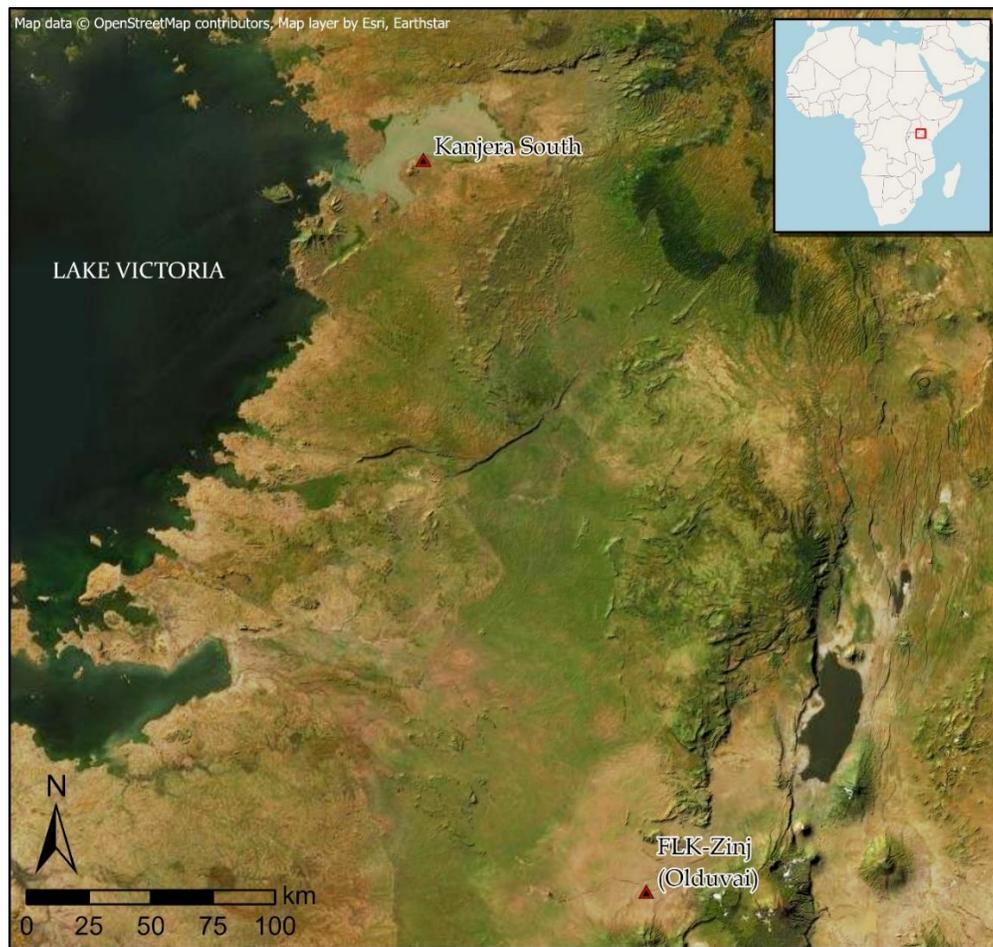
Strategy	Trophic engagement	Access to carcass	Returns	Procurement costs	Planning requirements	Mortality profiles	Taphonomic signature	Relevant Oldowan references
Facultative scavenging	Passive	Secondary	Meat scraps and within-bone nutrients	Low: late access to carcasses reduces initial competition	Low	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)

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

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

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

423 Carcass acquisition strategies at Early Pleistocene sites are frequently assessed
424 taphonomically, but limited faunal preservation or a lack of a clear association with co-occurring
425 lithic assemblages often prevent an accurate assessment of hominin behavior (Domínguez-
426 Rodrigo, 2009). Nonetheless, it may be possible to demonstrate a relationship between resource
427 exploitation strategies, seasonality, and the nature of lithic assemblages at certain Oldowan sites,
428 such as Kanjera South, Kenya (2.0 Ma), and FLK-Zinj (FLK Level 22), Olduvai Gorge, Tanzania
429 (1.84 Ma; Bunn, 1981; Bunn and Ezzo, 1993; de la Torre and Mora, 2005; Braun et al., 2009b;
430 Domínguez-Rodrigo, 2009; Ferraro et al., 2013; Parkinson, 2013; Oliver et al., 2019; Figure 1).



431
432 **Figure 1.** Map depicting the location of FLK-Zinj and Kanjera South, the two main Oldowan case-
433 studies discussed in the paper.

434 In terms of the lithic assemblages, Kanjera South frequently evidences bifacial centripetal
435 schemes, including on relatively large flakes, while 28% of the raw materials exploited were
436 selectively transported >10 km from conglomerates in the neighboring Awach drainage basin
437 (Braun et al., 2008; Braun et al., 2009a; Braun et al., 2009b). This may also be reflected in the
438 underrepresentation of cores in relation to flakes at the site, suggesting cores were transported into
439 the site for flake production, and then removed from the site for future use (Plummer and Bishop,
440 2016). Unidirectional unifacial methods were often restricted to local fenitized Nyanzian rhyolites
441 or dacites and Homa limestone or phonolite of poorer quality (Braun et al., 2009a; Reeves et al.,
442 2021), with transported materials being more heavily worked, and were selected according to the
443 durability of their cutting edge over flaking predictability (Braun et al., 2009a; Braun et al., 2009b;
444 Reeves et al., 2021). Flakes from these non-local raw materials also occasionally display secondary
445 retouch, something that is extremely rare for the Oldowan (Plummer and Bishop, 2016; Gallotti,
446 2018). These patterns of relatively long-distance transport and elongated reduction sequences are
447 suggestive of a considerable planning of activity across the landscape, potentially related to
448 predictability of resource exploitation.

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

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

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

466

467 *4.1. Kanjera South*

468 The site of Kanjera South (western Kenya) is centrally located within the northern margins
469 of the alluvial fans that cover the carbonatite geology of the Homa Peninsula, by the shore of
470 Winam Gulf, Lake Victoria (Behrensmeyer et al., 1995; Plummer et al., 1999; Plummer and
471 Bishop, 2016). The presence of lithic and faunal remains in the colluvial and alluvial silts and
472 sands of beds KS1–3 has been dated to 2.30–1.92 Ma through magneto- and bio-stratigraphy
473 (Ditchfield et al., 2019). The gentle nature of the deposition and the high sedimentation rates at
474 the lake margin, as suggested by minimal bone weathering and absence of both fluvial rounding
475 and debris-flow accumulations, favored the good preservation of archeological remains (Ditchfield
476 et al., 2019). The primary context of the site is further reinforced by the existence of several artifact
477 refits and the diversity of skeletal parts with differing water transport potential (Plummer et al.,
478 2009; Parkinson, 2013). The recurrent sedimentation cycles have afforded researchers an
479 opportunity to explore the nature of Oldowan hominin behavior through the time-lapse represented

480 in the KS1–3 beds, since humans were the primary biotic agent responsible for the accumulation
481 of archeological materials (Ferraro et al., 2013). Another interesting paleoecological component
482 of the Kanjera ecosystem is the predominance of open C₄ grassland habitats, alongside some
483 indications of woodland/grassland ecotones and a permanent watercourse, as inferred from the
484 $\delta^{13}\text{C}$ values of soil carbonates and herbivore enamel (Plummer et al., 2009). This existence of
485 nearby watercourses is reinforced by the presence of water-dependent taxa, such as hippotamids,
486 crocodylians, and reduncine bovids, although they are relatively rare in the sequence (Oliver et al.,
487 2019). The stability of resource exploitation strategies throughout the three archeological levels at
488 Kanjera South attests to the consistently productive nature of the landscape and repeated seasonal
489 attraction of the site over hundreds or even thousands of years (Ferraro et al., 2013; Lemorini et
490 al., 2014; Ditchfield et al., 2019).

491 In terms of zooarcheological data, the Kanjera South assemblage shows an even
492 representation of skeletal part profiles for small bovids (e.g., *Antidorcas* sp., *Gazella granti*), which
493 indicates procurement and processing of whole carcasses. In relation to the mortality profiles,
494 dental eruption and epiphyseal fusion rates suggest that a high proportion (50%) of both size 1–2
495 and size 3 bovids were young or subadult at the time of death (Parkinson, 2013; Plummer and
496 Bishop, 2016; Oliver et al., 2019; Table 3). The anatomical distribution of bone surface
497 modifications indicates that hominins had early access to the small prey size carcasses (Parkinson,
498 2013). The presence of cut-marks on small bovid remains, such as a metatarsal (KJS 7472) or the
499 proximal epiphysis of a femur (KJS 2565), is associated with limb disarticulation (Ferraro et al.,
500 2013), with the restricted intensity and frequency of carnivore damage indicating an only
501 occasional incidence of secondary scavenging (Parkinson 2013; Plummer and Bishop 2016). This
502 aligns well with the conclusions of Oliver et al. (2019) that the accumulation of size 1–2 bovids in

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

505

Bovoid 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

506 Abbreviations: MNI = minimum number of individuals.

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

509 We can better understand the seasonal relevance of the Kanjera South mortality profiles by
 510 using analogues derived from extant bovid ecology (Foley, 1983). The temporality and
 511 synchronicity of African bovid births are considerably variable, based on the timing of food supply
 512 growth (in relation to both protein peak and overall biomass), the length of time food is available,
 513 and anti-predator behavior exhibited (Jarman, 1974; Rutberg, 1987; Ims, 1990; Sinclair et al.,
 514 2000; Kingdon, 2015). According to Sinclair et al. (2000), most small bovid species living in small
 515 groups with non-precocial calves give birth during the wet season, although they do not exhibit a
 516 high degree of birth synchronicity. *Gazella* spp. for example, tend to produce their young early in
 517 the wet season, ahead of the high protein peak (Sinclair et al., 2000). In contrast, bovids living in
 518 larger herds with precocial young tend to have more tightly synchronized birth periods (Sinclair et
 519 al., 2000). Of particular relevance to the Kanjera South zooarcheological assemblage —where
 520 Alcelaphini (3a) play an important role (Ferraro et al. 2013; Oliver et al. 2019)—topi (*Damaliscus*
 521 *lunatus*) births also tend to peak around the onset of the wet season (Sinclair et al., 2000). As such,
 522 the number of juveniles from a range of bovid species is likely to peak during the wet season

523 (Pereira et al., 2014; Kingdon, 2015). This abundance makes them a paramount seasonal resource
524 that is most frequently exploited by omnivorous, rather than obligate, carnivores (Pereira et al.,
525 2014).

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

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

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

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

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

583 With regards to post-cranial within-bone nutrients, Parkinson (2013) notes that percussion
584 marks in the entire bovid assemblage are predominantly found on tibiae (c.40%)—the highest-
585 ranked bone for marrow extraction in terms of calorific output (Blumenschine and Madrigal,
586 1993)—while their overall count across all main long limb bones is low ($n = 15/6\%$, consistent
587 with the 6–9% values on midshaft fragments reported by Ferraro et al., 2013). This pattern of low
588 percussion mark counts despite high bone fragmentation might have been caused by a breakage
589 pattern in which hominins broke the bones against an anvil (Oliver, 1992; Parkinson, 2013).
590 Nonetheless, the low emphasis on within-bone nutrients of limb bones at the site may have also
591 been related to the seasonal temporality of marrow fat depletion (Sinclair, 1975; Speth, 1987;

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

596 The overabundance of isolated cranial and mandibular remains seems to suggest a
597 preferential transport of these elements to the site, with the presence of clear percussion striae
598 confirming that hominins targeted the consumption of their contents (Ferraro et al., 2013). The
599 excess cranial elements in proportion to post-cranial MNI counts may imply a different
600 procurement strategy, perhaps involving some extent of scavenging on skeletal parts left
601 untouched by primary predators (Ferraro et al., 2013; Oliver et al., 2019). Alternatively, their
602 presence may reflect the selective exploitation of natural deaths derived from late dry season
603 carrion pulses, and/or the hunting of these animals primarily to target their crania and mandibles
604 before an early abandonment of the rest of the fat-depleted carcass. Regardless, the procurement
605 and exploitation of cranial remains would be consistent with an attempt to maximize consumption
606 of fatty and energy-dense animal resources, such as brain matter and the mandibular nerve and/or
607 marrow (Blumenschine, 1987; Speth, 1987; Cordain et al., 2000; Ferraro et al., 2013). Since fatty
608 brain tissue contains one of the lowest protein percentages of any animal tissue (Jayathilakan et
609 al., 2012), their consumption would have assisted Kanjera South hominins in avoiding the ‘protein
610 ceiling’. The behavioral patterns inferred for the hominins at Kanjera South can be integrated into
611 a coherent animal exploitation strategy using insights from observations of modern hunter-
612 gatherers. In their ethnoarcheological study of a Kua rainy season camp (//oabe I)—occupied by
613 14 people for 7 nights—Bartram et al. (1991) noted that all nine ungulates procured were juvenile
614 or neonatal, easily obtained once their hiding places were located, and the juvenile carcasses were

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

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

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

638 (McGrew et al., 1979; Goodall, 1986; Stewart and Piel, 2014; Hicks et al., 2019; Pascual-Garrido
639 and Almeida-Warren, 2021). The Hadza also use wooden digging sticks to access USOs (Vincent,
640 1985). While preservation of wood is rare in the archeological record, recent finds from
641 Gantangqing, China, indicate that hominins in subtropical environments were (seasonally)
642 manufacturing such pointed implements and using them to obtain USOs, at least by the Late
643 Middle Pleistocene (Gao et al., 2021). Investment in the production of wooden implements at
644 Kanjera South is consistent with an attempt to minimize acquisition and processing costs of a
645 desirable and predictable resource to maximize return yields (Ferraro, 2007; Clark and Linares-
646 Matás, 2020). Although similar use-wear analyses at other sites are required for comparative
647 purposes, we suggest that plant resource exploitation at this site may have played a greater role in
648 governing the intensive exploitation of raw materials and the movement of lithics throughout the
649 landscape than is conventionally discussed in the Oldowan literature.

650

651 *4.2 FLK-Zinj*

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

661 freshwater wetland at Olduvai (Ashley et al., 2009; Ashley et al., 2010; Domínguez-Rodrigo et al.,
662 2010). This ecological setting would have been extremely attractive to dehydrated herbivores
663 throughout the dry season—and by extension to hominins and carnivores, due to both their needs
664 for drinking water and the opportunities for the active procurement of prey (Speth and Davis, 1976;
665 Domínguez-Rodrigo et al., 2010; Hawkes, 2016; Domínguez-Rodrigo et al., 2019a).

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

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

694 The taxonomic composition of the FLK-Zinj anthropogenic faunal assemblage mostly
695 reflects local, non-migratory species, such as *Kobus*, *Antidorcas*, and *Parmularius* (Domínguez-
696 Rodrigo et al., 2019b). Springbok (*Antidorcas* sp.) dominates the small-medium (size 1–2)
697 assemblage, while waterbuck (*Kobus* sp.) is the most common amongst the size 3 bovids (Bunn
698 and Pickering, 2010). Nowadays, migratory taxa (i.e., wildebeest [*Connochaetes gnou*]) are
699 present in the Olduvai landscape mostly during the short wet season (Domínguez-Rodrigo et al.,
700 2019b), although resident subpopulations may remain in the region year-round. Thus, if these
701 actualistic patterns are relevant for understanding Early Pleistocene paleoecological patterns, the
702 underrepresentation of migratory taxa would primarily suggest a dry season occupation
703 (Domínguez-Rodrigo et al., 2019a). Models of calorific return from the marrow of different long
704 bones at FLK-Zinj suggest that the exploited animals had suffered only very limited fat depletion
705 (Blumenschine and Madrigal, 1993). This observation would also be consistent with a broadly dry
706 season occupation.

707 While sample sizes are currently small, meso-wear and micro-wear patterns on ungulate
708 teeth from the site suggest that the anthropogenic components of the FLK-Zinj assemblage likely
709 formed during a single seasonal occupation, in contrast to the carnivore-accumulated Olduvai
710 assemblage of FLK-N, which reflects more prolonged periods of carcass acquisition throughout
711 the year (Domínguez-Rodrigo et al., 2019b). The tooth wear pattern could also represent repeated
712 occupations in the same season over time, but the limited subaerial weathering documented on
713 bone surfaces is more suggestive of relatively rapid sedimentary deposition (Domínguez-Rodrigo
714 et al., 2007; Domínguez-Rodrigo et al., 2019b). Waterbuck teeth, the best-represented size 3 bovid
715 at the site, exhibit a microwear pattern consistent with a mixed feeding diet (Domínguez-Rodrigo
716 et al., 2019b). This pattern would better fit the dry season dietary preferences of waterbuck, since
717 reduncines tend to follow a predominantly grazer regime during the wet season (Child and Richter,
718 1969; Herbert, 1972; Spinage, 1982; Gagnon and Chew, 2000; Kassa et al., 2007). Assuming FLK-
719 Zinj was indeed primarily occupied during the dry season, we suggest that procurement of
720 terrestrial animal resources, including meat, should represent an important part of the dietary
721 strategy at the site.

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

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

Bovoid 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

734 Abbreviations: MNI = minimum number of individuals.

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

737 Large bovid procurement strategies at FLK Zinj have been variously interpreted as evidence
 738 of selective ambush hunting (e.g., Bunn and Pickering, 2010; Domínguez-Rodrigo and Pickering,
 739 2017), non-selective (living structure), ambush hunting resembling Hadza and Kua practices
 740 (Bunn and Gurtoy, 2014), passive scavenging of felid-exploited carcasses (e.g., Blumenschine et
 741 al., 2012; Pante et al., 2015), confrontational scavenging of carnivore kills (e.g., Bunn, 2001; Bunn,
 742 2007; O'Connell et al., 2002), or exploitation of carrion pulses (Capaldo and Peters, 1995; Lim,
 743 2008). These strategies have also been evaluated with taphonomic evidence for hominin
 744 engagement with the carcasses, as well as the mortality profiles of the large bovid remains. With
 745 regards to the latter, the age profiles reported by Bunn and Pickering (2010) show a predominance
 746 of prime-aged individuals (12/20; 60%), with the proportion increasing to 77.8% (7/9) for
 747 waterbuck (*Kobus sigmoidalis*, size 3b).

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

759 The proposal of a marginal and passive interaction with exploited and abandoned carnivore
760 kills is undermined by evidence for recurrent early hominin access to the flesh of these
761 medium/large animals (e.g., Domínguez-Rodrigo et al., 2007; Parkinson, 2013). Both femora and
762 radio-ulnae show dense clusters of cut-marks in ‘hot zones’ (cf., Domínguez-Rodrigo, 1999),
763 demonstrating that hominins had primary access to fleshed carcasses (Oliver, 1994; Parkinson,
764 2018). Confrontational scavenging has been proposed as one way of reconciling evidence for
765 primary access without implying hominin hunting, since carnivore kills were a recurrent feature
766 of the Olduvai Bed I paleolandscape (Bunn and Kroll, 1986; Bunn, 2001; O’Connell et al., 2002)
767 and carnivore predation is a major source of mortality for medium-sized ungulates in the Serengeti
768 (Sinclair et al., 2003). These suggestions are, however, also difficult to reconcile with the cut-mark
769 distribution data discussed above, since the same elements of size 3 bovids with abundant cut-
770 marks at FLK-Zinj tend to be defleshed quickly by lions (O’Connell et al., 1988b; Domínguez-

771 Rodrigo, 1999; Bunn and Pickering, 2010; Gidna et al., 2014). Furthermore, the mortality profiles
772 of lion kills are significantly different to that seen at FLK-Zinj, and the penecontemporaneous site
773 of DS, as the former tend to include substantially fewer prime adults (Bunn and Pickering, 2010;
774 Bunn and Gurtoy, 2014; Cobo-Sánchez, 2020). Lastly, studies on the behavioral ecology of
775 carnivore predation have shown that extant lions tend to preferentially target larger prey sizes when
776 they are available, especially buffalo (size 4), across a range of ecosystems (Funston and Mills,
777 2006; Davidson et al., 2013; Dublin and Ogutu, 2015). This contrasts with the predominance of
778 size 1–3b bovids in anthropogenic Olduvai Bed I assemblages (Bunn and Pickering, 2010; Cobo-
779 Sánchez, 2020), further emphasizing that large felids were unlikely to have been the main agent
780 of accumulation at FLK-Zinj.

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

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

795 In addition to the zooarcheological and taphonomic data, actualistic insights from bovid
796 ecology can help elucidate further the nature of hominin carcass acquisition at the site. Since *Kobus*
797 *sigmoidalis* is the most abundant size 3 bovid at FLK-Zinj (Bunn and Pickering, 2010), we center
798 our discussion around it. This extinct waterbuck species is similar in size and phenotype to the
799 extant *Kobus ellipsiprymnus* in East Africa, presumably occupying similar habitats (Spencer,
800 1997). The species is gregarious and non-migratory (Foley, 1983), living in groups of 6–30
801 individuals. Waterbuck stay near active water sources, particularly during the dry season, since
802 waterbuck do not tolerate dehydration well (Taylor et al., 1969; Foley, 1983; Estes, 2004).

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

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

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

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

848 We also suggest that dry season hunting patterns may have played a role in the expedient
849 nature of the lithic toolkit at FLK-Zinj, suggested by the overall predominance of relatively simple
850 unidirectional and unifacial reduction schemes and the lack of retouch on flakes (de la Torre and
851 Mora, 2005; Gallotti, 2018). Our seasonality framework would suggest that the meat and within-
852 bone nutrients of terrestrial ungulates were important resources for hominins throughout most of
853 the dry season, as they are for the Hadza (Bunn et al., 1988; Hawkes et al., 1991; O’Connell et al.,
854 1992; Marlowe and Berbesque, 2009). Future use-wear analysis will help to test this at FLK-Zinj
855 (cf., Bello-Alonso et al., 2019). Nevertheless, successful carcass acquisition endeavors may have
856 been rather unpredictable at the daily scale (Hawkes, 2000), making it more difficult to time the
857 use of tools throughout the landscape. In this context, we note the finding of Binford (1979) that
858 the lithics produced by the Nunamiut for an immediate need were notably less complex than those
859 used in pre-planned activities. Moreover, Kua hunter-gatherer groups in the Kalahari tend to
860 consume carcasses almost immediately during the hot dry season, and transport them only across

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

865 The butchery activities documented taphonomically at FLK-Zinj heavily emphasize filleting
866 rather than disarticulation (Parkinson, 2018), and slicing meat offers little resistance to lithics
867 (Bello-Alonso et al., 2019). As such, the task can be achieved as successfully with unretouched
868 than with retouched flakes (Jones, 1994), thus discouraging the additional investment required by
869 the latter. That lithics and faunal remains at FLK-Zinj are functionally associated is further
870 supported by their correlated spatial distributions (Domínguez-Rodrigo and Cobo-Sánchez, 2017).
871 Risk-buffering processes may also explain investment in directional quartzite transport into the
872 site from the Naibor Soit, rather than use of the local lava cobbles which predominate in Leakey's
873 (1971) unmodified manuports (de la Torre and Mora, 2005). Quartzite flakes display greater initial
874 edge sharpness despite their reduced durability, and thus its selection suggests a desire to maximize
875 efficiency in short-term tasks (Key et al., 2020). In this context it is interesting to note that such a
876 preference for quartzite over basalt flakes (and handaxes) is directly associated with butchery
877 practices at the Bed II sites of FLK-W and BK (Yravedra et al., 2017a; Yravedra et al., 2017b).
878 Hominins were thus likely to have been planning their repeated visits to the site following
879 acquisition of carcasses during the dry season (Domínguez-Rodrigo et al., 2010). This behavioral
880 scheduling would have provided an opportunity to minimize the costs of transporting quartzite
881 across the landscape during hunting forays by maintaining a raw material presence at a known
882 processing spot, and quickly producing usable flakes when carcasses were brought to the site (cf.,
883 Potts, 1984; Potts, 1991).

884 **5. Discussion**

885 *5.1. Seasonality and Oldowan behavioral flexibility at Kanjera South and FLK-Zinj*

886 As outlined above, we argue that the available data from Kanjera South (Kenya) and FLK-
887 Zinj (Olduvai Gorge, Tanzania) evidence a pattern of seasonal variation in Oldowan subsistence
888 strategies, which underscores the behavioral flexibility of early *Homo*. The term ‘behavioral
889 flexibility’ has a long history of use in relation to animal learning and adaptation in the fields of
890 behavioral psychology and behavioral ecology (e.g., Dickinson, 1981; Kummer and Goodall,
891 1985; Tebbich et al., 2010; Navarrete et al., 2016; Audet and Lefebvre, 2017). The term is used
892 here simply to highlight the problem-solving skills of Oldowan hominins, for whom seasonal shifts
893 would have constantly re-structured acquisition priorities on the basis of resource quality and
894 availability.

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

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

908 Meanwhile, carcass processing at Kanjera South was generally less intensive than at FLK-
909 Zinj, both in terms of defleshing and limb bone marrow processing (Domínguez-Rodrigo et al.,
910 2007; Ferraro et al., 2013; Parkinson, 2013; Parkinson, 2018). Instead, hominins at Kanjera South
911 preferentially targeted the brains and/or cranial pulp of large bovid skulls as well as mandibular
912 nerve and marrow (Ferraro et al., 2013), resources that would have maintained a greater fat content
913 into the early wet season (Sinclair, 1975). In this context, we suggest that activities enabling access
914 to consistently fat-rich resources, such as evisceration and brain extraction, would have been
915 particularly important during these periods of ungulate depletion. In contrast, the utility of
916 defleshing and marrow extraction would have been much greater when bovid fat stores were more
917 substantial. We also speculate that disarticulation may have been more relevant throughout the wet
918 season as a whole, as ungulate dispersal and hominin movement through the landscape were
919 generally more extensive. Nonetheless, we note that ethnoarcheological assessments of differential
920 body part transport by animal condition (pregnant, juvenile, feeble) or season of acquisition are
921 limited by small sample sizes (Lupo, 2006), meriting further research.

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

929 Blumenschine and Marean, 1993) alongside low tooth mark (5.4%) and percussion mark values
930 (7.8%). The proportion of midshaft fragments with percussion marks closely mirrors the 6–9%
931 values reported for Kanjera South and are well below those from FLK-Zinj (Ferraro et al., 2013;
932 Parkinson, 2018). This relatively limited engagement with within-bone nutrients occurs alongside
933 cut-marked hippopotamid remains, a considerable number of shed crocodile teeth (Pante et al.,
934 2018), and a notable concentration of fish remains suggesting a catastrophic mortality episode
935 (Bibi et al., 2018). This mortality profile is expected from modern observations of fish becoming
936 trapped in pools as the water recedes in the late dry season (Leakey, 1971; Stewart, 1994). Extant
937 crocodiles also tend to congregate within increasingly isolated pools of water towards the end of
938 the dry season (Njau, 2012), a time they are known to share them with hippopotami (Kofron,
939 1993). This suggests an occupation of LAS at HWK-EE that encompassed the very late dry season,
940 which would be consistent with the more general dry season indication given by bovid tooth micro-
941 and meso-wear data (Rivals et al., 2018).

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

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

961 **Table 5:** Summary of predictions discussed in the text for assessing seasonality of site use in the
962 Oldowan, derived from the comparison of Kanjera South and FLK-Zinj and incorporating insights
963 from other Early Pleistocene localities discussed in the text. Presence or absence of migratory taxa
964 may also be a relevant seasonal, landscape-specific paleoecological signature. Note that hominin
965 occupation at some Oldowan sites may span more than one season or a seasonal transition
966 (potentially including FwJj20), while natural site formation processes may also result in the
967 deposition of background material from successive seasons. With regards to assessments of
968 mortality profiles, skeletal part profiles, and spatial distribution of faunal remains, it is important
969 to consider the impact of secondary carnivore ravaging, post-depositional transport, and bone
970 preservation biases due to biogeochemical processes. Any of these factors would compromise the
971 integrity of the faunal assemblage, making inferences regarding the specific nature and intra-
972 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
	Early wet season	Abundance of bovid juveniles Catfish in fluvial contexts	Emphasis on head contents Limited emphasis on meat and marrow		Greater use-wear emphasis on plant processing

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

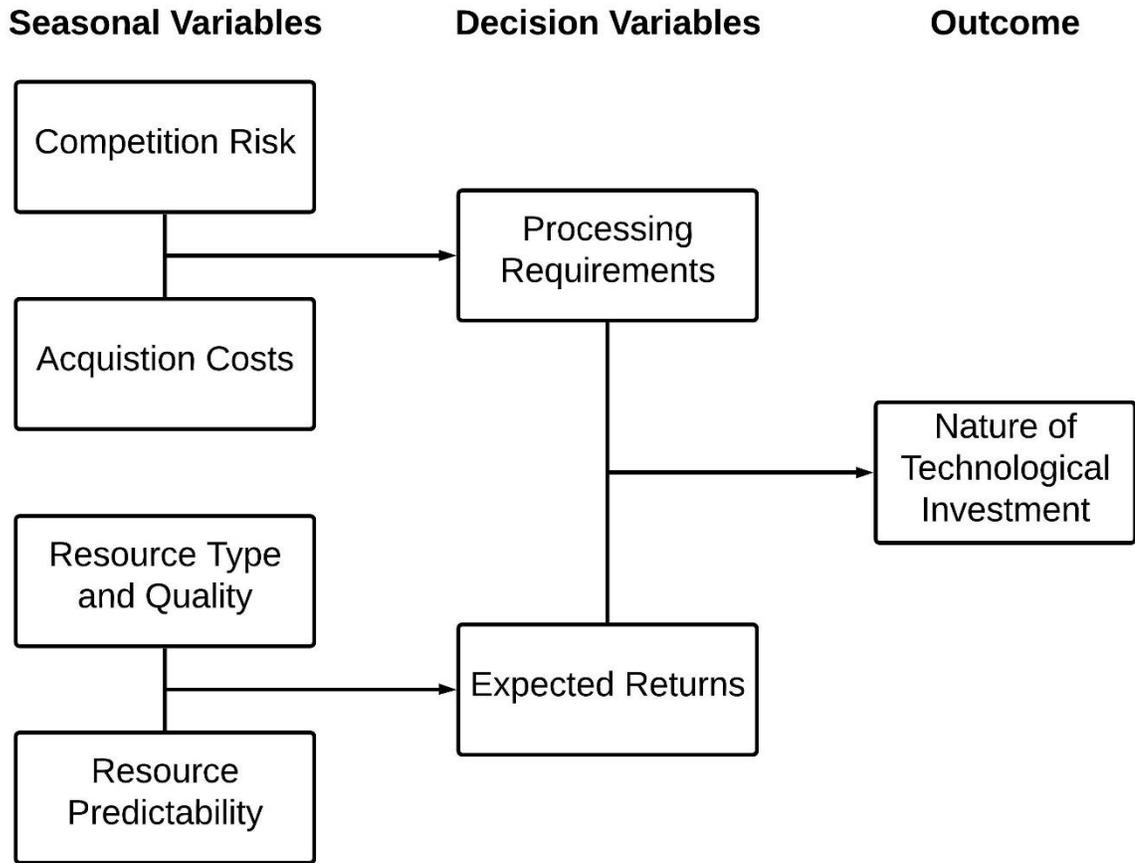
987 The prevailing character of the FLK-Zinj lithic assemblage is one of expediency, as indicated
988 by the predominance of unifacial, unidirectional reduction strategies, and only very limited
989 secondary retouch (Leakey, 1971; de la Torre and Mora, 2005; Gallotti, 2018). Some of this
990 reduced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

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

1000 This contrasts with the pattern at Kanjera South, where selection of materials emphasized
1001 durability over flaking predictability (Braun et al., 2009a). Had Kanjera South shared a similar
1002 emphasis on the fast production and use of raw material with FLK-Zinj, we would have expected
1003 flaking predictability to have been a more important factor in the knapping of material. Instead,
1004 the hominins at the site were willing to accept a greater risk of shorter flakes with less sharp edges
1005 and a greater chance of hinge and step fractures in order to produce more durable cutting edges
1006 (Braun et al., 2009a). This emphasis on tool durability at Kanjera occurs alongside the
1007 aforementioned increased frequency of investment in reduction (particularly bifacial centripetal
1008 reduction schemes), producing longer cutting edges relative to flake mass, and in secondary
1009 retouch, with certain raw materials being transported into the site from >10 km away (Braun et al.,
1010 2008; Braun et al., 2009a; Braun et al., 2009b; Reeves et al., 2021). This implies a decoupling of
1011 lithic use from specific points on the landscape (cf., Braun and Harris, 2003). In addition, non-
1012 local materials at Kanjera tend to be among the most durable, and show the most retouch (Braun
1013 et al., 2009a; Braun et al., 2009b; Lemorini et al., 2014), a technological strategy that would have
1014 enhanced further the potential use-life of the tools (Jones, 1981). This trade-off implies that
1015 hominins were planning more abrasive or time-consuming activities such as skinning and/or the
1016 processing of medium-hard plant tissues (Braun et al., 2009a). Indeed, use-wear evidence at
1017 Kanjera South confirms that a substantial quantity of lithic implements were primarily devoted to
1018 the processing of plant resources (Lemorini et al., 2014; Lemorini et al., 2019). Recent
1019 experimental studies have shown that flake retouch and larger flake sizes, which increase force

1020 loading and manipulability, enhance wood processing efficiency, suggesting that plant resource
1021 manipulation directly influences lithic investment (Bencomo Viala et al., 2020; Gürbüz and Lycett,
1022 2021). These patterns may reflect the establishment of a processing chain to enhance resource
1023 procurement through organic tool use (cf., Pascual-Garrido and Almeida-Warren, 2021).

1024 We use these observations as an empirical basis from which to develop predictions regarding
1025 the relationship between seasonality and technological investment in the Oldowan. According to
1026 evolutionary optimality theory, organisms attempt to maximize a particular currency variable, such
1027 as nutrient return rates, with decisions made according to the costs and benefits of a particular
1028 action, in the context of available constraints (Hawkes et al., 1982; Foley 1985; Stephens and
1029 Krebs, 1986; Winterhalder and Smith, 1992; Ferraro, 2007; Kelly, 2013). In this context, we
1030 emphasize the relevance of seasonal variables, such as competition risk, resource type and quality,
1031 acquisition costs, and resource predictability, for understanding the level of expected technological
1032 investment in lithic assemblages. In Figure 2, these seasonal variables can be considered intra-
1033 annual constraints on technological development, informing the relative costs (processing
1034 requirements) and benefits (expected returns) on such investment.



1035

1036 **Figure 2.** Expected relationship between resource seasonal resource procurement and
 1037 technological outcomes in the context of Oldowan.

1038 Faunal acquisition during the Oldowan relied on the relatively unpredictable exploitation of
 1039 sparse and mobile resource patches, at least partially through compensatory hunting at both
 1040 Kanjera and FLK-Zinj. The use of such hunting strategies is likely to have reduced the
 1041 unpredictability of return yields associated with other carcass acquisition strategies, but it still
 1042 would not have approached the predictability of distribution and returns seen in plant resources,
 1043 particularly during the wet season. Indeed, modern observations of the Hadza suggest men only
 1044 succeed in obtaining large carcasses in 1 in 30 hunter-days, remaining as low as 1 in 3 when small
 1045 game hunting and trapping was carried out (Hawkes et al., 1991; Hawkes et al., 2001). Given that
 1046 Oldowan hominins lacked the technological complexity observed in the Hadza, particularly bows

1047 and arrows, we can envisage even greater failure rates in the Early Pleistocene. Furthermore,
1048 experimental studies have suggested that retouched flakes are not more effective in this task than
1049 unretouched flakes (Jones, 1994), suggesting that increased investment for predominantly
1050 defleshing purposes will not always produce a corresponding dietary return. In this context, returns
1051 on investment towards carcass processing beyond expedient unretouched flakes upon procurement
1052 would have been minimal relative to costs and relatively unpredictable. Furthermore, the
1053 spatiotemporal co-occurrence of hominins and carnivores in the ecosystem during the dry season
1054 demanded the evaluation of trade-offs between defending or abandoning a carcass before complete
1055 exploitation. Time constraints associated with predation risk have been suggested to directly
1056 influence lithic reduction sequences and Oldowan tool use at Swartkrans, South Africa (Caruana,
1057 2020). Taken together, we would expect a greater emphasis instead on an expedient flake toolkit
1058 capable of fast carcass processing in dry season contexts, as observed at FLK-Zinj.

1059 In contrast, investment in increased handling efficiency is most effective when search costs
1060 are minimal in relation to time spent harvesting and processing a resource (Hawkes and O'Connell,
1061 1992; Hawkes et al., 2018). In the context of increased plant availability and diversity in the wet
1062 season (Sept, 1984), knowledge regarding the abundance and predictability of visible and
1063 embedded resource distributions may have minimized search times and reduced resource
1064 procurement competition (cf., Foley, 1985; Clark and Linares-Matás, 2020). In addition, given the
1065 greater energy density of animal resources (particularly fat: 9 kcal/gram), plant carbohydrates will
1066 generally produce lower caloric return per unit of weight (4 kcal/gram) and unit of handling time
1067 (US National Research Council on Diet and Health, 1989; Stewart, 2014). This further elongates
1068 the required amount of time spent handling these resources to meet caloric requirements (Hawkes
1069 et al., 1982). These factors would have fostered investment towards minimizing handling costs

1070 and maximizing overall return rates, while also allowing for the ability to foreplan the use of lithic
1071 technology throughout the landscape (Clark and Linares-Matás, 2020). Taken together, we would
1072 therefore expect greater investment in raw material selection and transport (where high-quality
1073 local materials are not available) at wet season sites. This should result in a corresponding increase
1074 in lithic reduction intensity and in the diversity of final forms, including an extent of secondary
1075 retouch. We argue that these patterns are reflected in the relative lithic complexity observed at
1076 Kanjera South (Braun et al., 2009b; Lemorini et al., 2014; Reeves et al., 2021).

1077

1078 *5.2. Seasonality and habitat selection in the Oldowan*

1079 A recent comparison of faunal exploitation between Kanjera South and FLK-Zinj
1080 emphasized that the affordances of different habitat types, such as grasslands and woodlands,
1081 heavily influenced specific modes of hominin resource acquisition (Oliver et al., 2019). While this
1082 is certainly true, seasonal constraints and opportunities would have actively influenced Oldowan
1083 habitat selection patterns. Predictable response patterns to seasonality-mediated changes in habitat
1084 composition, suitability, and the spatial distribution of preferred resources have been documented
1085 for a wide range of genera across a diversity of heterogeneous ecosystems (e.g., Fleming et al.,
1086 1987; Van Schaik et al., 1993; Pape and Löffler, 2015; Vélez et al., 2017; Stanley et al., 2021),
1087 including chimpanzees in forest-woodland mosaic environments (Collins and McGrew, 1988;
1088 Pennec et al., 2020). Moreover, modern human hunter-gatherers show clear patterns of seasonal
1089 movement, with camps tending to be located near perennial water sources during the (late) dry
1090 season (e.g., Hawkes et al., 1997; Lee, 2013). Among the Hadza, wet season camps are more
1091 ephemeral, with repeated camp movement determined by relatively frequent fluctuations in the
1092 spatio-temporal distribution of berries and honey (Hawkes et al., 1997).

1093 We argue that predictable fluctuations in the spatio-temporal distribution of resources would
1094 have encouraged Oldowan groups to schedule their food-procurement strategies, technological
1095 investment, and preferred habitats on the basis of seasonal constraints and opportunities. The
1096 lakeshore grassland environment at Kanjera South would have enjoyed moist soils and ephemeral
1097 watercourses during the wet season (Ditchfield et al., 2019), which would have profound
1098 implications for plant resource availability and seasonal habitat attractiveness for Oldowan
1099 hominins and other animals. In the context of modern hunter-gatherer seasonal foraging strategies,
1100 the Hadza specifically target environments rich in berries, such as the floodplain of the Barai River
1101 near Lake Eyasi (Vincent, 1985), with the availability of these berries even dictating the location
1102 of many wet season camps (Hawkes et al., 1997). We also note that the probability of finding
1103 medium- to large-sized carcasses with scavenging potential during the wet season in the Serengeti
1104 increases along erosion embankments and the margins of riparian woodlands (Blumenschine,
1105 1987; Hopcraft et al., 2005). In contrast, the mosaic woodland with perennial springs around FLK-
1106 Zinj (Ashley et al., 2010) would have been an attractive dry season hotspot for ungulates,
1107 carnivores, and hominins seeking water and other resources (Hopcraft et al., 2005; Hawkes, 2016).

1108 We also emphasize that our proposed model regarding the nature of lithic investment at
1109 Oldowan sites may be reinforced by raw material management strategies in relation to the length
1110 of site occupation in the face of seasonal variability in habitat selection. In the context of the Late
1111 Pleistocene, Riel-Salvatore and Barton (2004) point out that longer-term occupation of a site,
1112 especially where raw material has been cached, should be associated with reduced intensity of
1113 reduction and curation, as the pressure on preserving raw material is lower. In turn, this should
1114 result in greater artifact densities at such a site, but with an overwhelming focus on unretouched
1115 flakes. Thus, site-level raw material provisioning in the context of a longer duration of

1116 occupation(s) near perennial water sources during the dry season may have contributed to the
1117 patterns observed at FLK-Zinj. In contrast, in contexts of higher mobility across the landscape and
1118 shorter occupations, hominins should be faced with greater constraints on raw material availability,
1119 resulting in a need to more efficiently utilize (transported) raw material through intensive core
1120 reduction and flake maintenance through edge retouch. This may relate to the technological
1121 patterns observed at Kanjera South (Reeves et al., 2021), in the context of wet season foraging
1122 activities.

1123

1124 *5.3. Seasonality and freshwater resource exploitation in the Oldowan*

1125 Terrestrial animal and plant resources were certainly not the only components of Oldowan
1126 diets. In particular, freshwater resources such as crocodiles, testudines, fish, or shellfish would
1127 have offered rich polyunsaturated and Omega-3 fatty acids, as well as trace minerals and vitamins
1128 (Stewart, 1994; Braun et al., 2010; Archer et al., 2014; Cáceres et al., 2017). These resources
1129 exhibit relatively predictable distribution patterns and availability peaks, being most easily
1130 captured during the very late dry and early wet seasons (Stewart, 1994), the periods when terrestrial
1131 animal resources would have been most fat-depleted. Furthermore, the intra-annual patterns of
1132 behavior in many freshwater taxa can act as important paleoecological information for inferring
1133 the seasonality of site formation.

1134 At Olduvai, the fish assemblages ($n = 4000$) of Bed I and II sites exhibit low taxonomic
1135 diversity, likely due to the high salinity and alkalinity values of the Olduvai paleolake (Greenwood
1136 and Todd, 1970; Stewart, 1994). At FLK-Zinj, the assemblage (number of identified specimens
1137 [NISP] = 110) comprises predominantly catfish (83.3%) and cichlids (16.7%; Stewart, 1994).
1138 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.,

1162 Sampson, 2000), while the presence of cut-marks on the ventral surface of a turtle costal carapace
1163 element indicates that evisceration was also being carried out on turtle carcasses (cf., Blasco, 2008;
1164 Braun et al., 2010). With regards to fish, the FwJj20 assemblage (NISP = 405) is dominated by
1165 catfish (NISP = 365, MNI = 49). The catfish skeletal part profiles show an over-representation of
1166 cranial fragments (ca. 75%; Stewart, 1994; Braun et al., 2010; Archer et al., 2014). Archer et al.
1167 (2014) notes that head over-representation is often the result of butchery processes, as further
1168 evidenced by the presence of cut-marks (mostly on cranial fragments), as well as intentional
1169 fragmentation. 25.5% of cranial fragments have green breakage planes—with 27.5% of these
1170 initiated along sutures—and 2.5% exhibit percussion marks and associated notches (Archer et al.,
1171 2014). On the basis of catfish butchery experiments engaging local Turkana fishing communities,
1172 cranial breakage along sutures using a hammerstone appears to be strongly associated with access
1173 to the fat-rich brain matter (Archer et al., 2014).

1174 Archer et al. (2014) suggest that the main drivers of hominin exploitation of freshwater
1175 resources may have been attempts to reduce energetic investment in resource acquisition, to reduce
1176 technological costs, or to reduce carnivore competition. Additionally, their exploitation may have
1177 been related to seasonal periods of animal depletion and diminishing body fat percentages (Archer
1178 et al., 2014). Carnivore tooth mark patterns on limb bone fragments at FwJj20 (1.9% NISP)
1179 indicates that carnivore competition in this riparian woodland setting (Bamford, 2011) was lower
1180 than at both the dry season mosaic woodland environment at FLK-Zinj or the wet season open
1181 grassland environment at Kanjera South. As such, rather than representing primarily an attempt to
1182 avoid carnivore competition, we concur that low procurement costs may have facilitated the
1183 seasonal exploitation of fat-rich freshwater resources by hominins. Hominins at FwJj20 appear to
1184 have exploited terrestrial animal resources rather selectively, given the evidence for evisceration

1185 and skeletal part selection through disarticulation alongside comparatively little evidence for
1186 terrestrial carcass filleting at the site (Braun et al., 2010). Similarly, percussion marks on terrestrial
1187 limb bones are low ($n = 4$), suggesting little emphasis on limb bone marrow nutrients of terrestrial
1188 animals (Braun et al., 2010: Table 2), confirming the overall signature of less intensive carcass
1189 processing than at FLK-Zinj. These taphonomic insights are consistent with a pattern of seasonal
1190 fat-depletion in the flesh and marrow of African ungulates (cf., Sinclair, 1975; Speth, 1987).

1191 On the basis of fish ecology, the reliance on catfish exploitation within a humid fluvio-
1192 lacustrine context at FwJj20 may also be used to infer seasonality of occupation, as the
1193 aforementioned catfish engage in mass riverine migration towards the onset of the early rainy
1194 season to spawn (Stewart, 1994). Intensive catfish exploitation in a fluvial context has also been
1195 reported at BK in Olduvai Bed II, and was used by Stewart (1994) to infer a very late dry to early
1196 wet season context, potentially allowing the same deduction to be applied to FwJj20. A hominin
1197 presence spanning this seasonal transition would also be consistent with the diverse
1198 paleoecological signatures observed at the site. For example, the high density of water-dependent
1199 reduncine remains and the co-occurrence of abundant crocodile and hippopotamid remains would
1200 indicate late dry season, while the high proportion of chelonid, in relation to bovid NISP values
1201 would be suggestive of wet season (cf., Speth and Davis, 1976). Embedded fish resources, such as
1202 the energy-dense head content of catfish, appear to have been particularly desirable to the FwJj20
1203 hominins (Archer et al., 2014). Since catfish brains have a similar metabolic composition to
1204 mammalian brains (Du et al., 2018), they likely performed a similar dietary function at FwJj20 to
1205 the large bovid heads and mandibles processed at Kanjera South (Ferraro et al., 2013) in the
1206 seasonal food-procurement schedules of early *Homo*. It is also possible that the cut-marks found
1207 on a crocodile skull fragment at Gona OGS-6 (Cáceres et al., 2017) may have similarly been

1208 produced during butchery processes that targeted within-head contents, in addition to adhering
1209 flesh. We anticipate that further publications on the technological sequences and use-wear of the
1210 lithics of FwJj20 will allow for more holistic comparisons with other Oldowan sites.

1211

1212 **6. Conclusions**

1213 In this paper, we have attempted to derive a framework for interpreting the influence of
1214 seasonality on hominin behavior within the Oldowan record, using patterns of resource
1215 consumption and lithic investment at FLK-Zinj and Kanjera South as a lens through which
1216 behavioral variability can be studied. On the basis of zooarcheological assessments of mortality
1217 profiles and the taphonomic evidence for early hominin access to carcasses, we argue that at least
1218 some extent of compensatory hunting is a shared feature of both sites. Nonetheless, there are
1219 differences in prey demographics that can be related to seasonal cycles of vulnerability, matching
1220 expectations derived from actualistic observations of carnivore feeding behavior (Owen-Smith,
1221 2008; Pereira et al., 2014; Arriaza et al., 2015). The ability to achieve primary access to terrestrial
1222 ungulates in different seasons may be indicative of novel foraging behaviors that enhanced overall
1223 resource yields from patchy resources. Late Oldowan hominins may have relied on social networks
1224 to identify and pursue carcass acquisition opportunities, while keeping predators away in the
1225 process. At the same time, we emphasize that the relative relevance of certain animal resources in
1226 Oldowan diets was a distinctly seasonal phenomenon. For example, fat-depleted meat would have
1227 been less attractive during periods of nutritional stress (cf., Speth, 1987), such as the very late dry
1228 season and the early wet season. In these contexts, energy-dense resources such as ungulate head
1229 contents, plant carbohydrates, nuts, and freshwater taxa would have been particularly desirable.

1230 We further argue that seasonal changes to food-procurement strategies, partially mediated
1231 through habitat selection, would have contributed to the patterning of techno-economic behavior.
1232 Embedded social landscape knowledge would have been an underlying requirement in hominin
1233 awareness of changing resource distribution patterns and the ability to successfully track and
1234 exploit those resources (Clark and Linares-Matás, 2020). Animal resource exploitation involving
1235 fast and comprehensive carcass processing upon procurement encouraged greater lithic
1236 expediency at dry season sites, especially when facilitated by raw material place provisioning, as
1237 interpreted for FLK-Zinj. In contrast, the nutritional constraints associated with the consumption
1238 of fat-depleted terrestrial animal resources during the very late dry season and the early wet season
1239 actively encouraged hominins to engage in the preferential selection of fat-rich skeletal parts, such
1240 as head contents, mandibular nerve and marrow, and viscerae. Freshwater aquatic resources would
1241 have also provided a source of fatty acids at this time of the year, as discussed in relation to FwJj20.
1242 The availability, predictability, and dietary relevance of plant resources during the early-mid wet
1243 season would have encouraged hominins to shift their overall dietary emphasis towards
1244 carbohydrate-rich plants. In this context, planning of subsistence behaviors through the landscape
1245 and investment in raw material transport and/or lithic reduction schemes may have allowed for
1246 reduced resource acquisition and processing costs, either directly or for the production of suitable
1247 tools on organic materials. We propose that these seasonal dynamics could help explain the
1248 archeological record of Kanjera South. We suggest that the consolidation and subsequent
1249 elaboration of these behavioral patterns allowed early *Homo* to more successfully negotiate
1250 seasonal variability in resource predictability and habitat structure from the Early Pleistocene
1251 onwards.
1252

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