

Taphonomic estimates of competition and the role of carnivore avoidance in hominin site use within the Early Pleistocene Olduvai Basin

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Abstract:

It has become increasingly clear among paleoanthropologists that Early Pleistocene sites sample a diversity of behaviors and no one model is sufficient to explain every collection of archaeological debris. With this comes the realization that hominins reacted to an equally diverse set of ecological parameters, each of which determined to some extent where, when, and how they chose to concentrate, or not concentrate, their activities across ancient landscapes. Competition with, and predation risk from, large carnivores is thought to be an especially critical factor, particularly when large mammal tissues became a component of hominin diets after 2.6 million years ago. Here, the degree to which carnivore avoidance influenced patterns of hominin site use is evaluated with a sample of faunal and lithic assemblages from Beds I and II at Olduvai Gorge, Tanzania. Multivariate measures of bone destruction, as proxies for levels of on-site competition and thus predation risk, show little systematic relationship with patterns of lithic discard and butchery. This suggests that while carnivore avoidance was probably part and parcel of hominin daily life in the Early Pleistocene Olduvai Basin, other considerations such as water, tree cover, dry land, and toolstone played more proximate roles.

Keywords: Olduvai Gorge | Early Pleistocene | carnivore competition | hominin diet

Article:

1. Introduction

It is probably safe to say that paleoanthropologists have moved beyond the rather simplistic view that Early Pleistocene archaeological sites, even the seemingly homogenous “living floors” (Leakey, 1971: 258) or “Type C” sites (Isaac, 1978: 95; Isaac and Harris, 1978: 77–78), can be characterized universally as either home bases or stone caches, as either central places or refuges. Researchers have in fact been implored to avoid such hazards for quite some time (Potts, 1994), and the persistence of any mutual exclusivity is probably as much an artifact of caricature by non-specialists as it is a reflection of the state of affairs among specialists. The temptation to treat sites as monolithic entities is nevertheless strong given that the inferred behavioral

correlates of various scenarios of site formation, be it active hunting, regular food-sharing, consistent transport of lithic and faunal material, parental provisioning, or a tightly bonded, family based social organization, set the baseline for what early stone tool using hominins were minimally capable of. This in turn has implications for broader themes in human evolution such as, for example, how (or if) lithic technology and carnivory ultimately paved the way for the development of extreme encephalization (Aiello and Wheeler, 1995), superlative colonization abilities (Antón et al., 2002, Foley, 2002, Wells and Stock, 2007), and a truly unique life history (Kaplan et al., 2000, Hill et al., 2009).

Having said that, behavioral flexibility was probably a key component of hominin adaptations, and it is possible, even likely, that they created *all* the site types identified by archaeologists and many more besides. Indeed, a growing body of work documents highly variable strategies of hominin land usage across penecontemporaneous paleolandscapes (Blumenschine and Masao, 1991, Bunn, 1994, Potts et al., 1999, Domínguez-Rodrigo et al., 2002, Braun et al., 2008, Blumenschine et al., 2012a). The goal then becomes to identify the parameters, or affordances (resources and hazards; *sensu* Peters and Blumenschine, 1995: 334), that conditioned where, when, and how hominins chose to concentrate their archaeologically visible behaviors across ancient landscapes. Water accessibility, tree cover, toolstone distribution, food (both plant and animal) availability, and competition and predation risk are the most typically cited affordances in studies of Early Pleistocene hominin ecology (Peters and Blumenschine, 1995, Blumenschine and Peters, 1998). The latter affordance is of particular interest in this context, as the tool-assisted butchery and consumption of carcasses thrust hominins into a diverse guild of African carnivores as would-be competitors and, potentially, increasingly susceptible prey (Turner, 1988, Shipman and Walker, 1989, Brantingham, 1998a, Brantingham, 1998b, Van Valkenburgh, 2001, Pobiner and Blumenschine, 2003).

The well-preserved sites from Olduvai Gorge, Tanzania, play a prominent role in reconstructions of competition and predation risk and their impact on the lives of early hominins. Potts, 1984, Potts, 1988, for example, argues that many of the Bed I sites were likely to have been dangerous areas, citing, among other things, the presence of complete limb bones as evidence for hurried and incomplete carcass processing by hominins intent on quickly vacating areas of high predation risk. Capaldo (1997), in his study of the gorge's most celebrated assemblage, that from Level 22 at the FLK locality (the “*Zinjanthropus* Floor”) points out that complete limb bones probably reflect a low competition setting, as unprocessed skeletal parts would not survive long with hungry consumers in the vicinity. He also notes that the fauna preserves axial and compact bones in much higher frequencies than seen among heavily ravaged carcasses in actualistic contexts, indicating only moderate carcass destruction and thus low levels of on-site competition and, presumably, predation risk (cf. Domínguez-Rodrigo and Organista, 2007, Domínguez-Rodrigo et al., 2010). In another study of the same collection, Faith et al. (2007) find no relationship between the survival of major long bone epiphyses and their density. They suggest that such a pattern is expected under conditions of intense competition, as carnivores will consume any and all parts they can get ahold of regardless of their density and grease/marrow yield. Blumenschine, 1991, Blumenschine et al., 1994: 205) offers what is probably the most comprehensive model, which is based largely on the expectation that hominins “should adopt behavioral strategies to acquire and process carcasses that minimize competition from carnivores.” Blumenschine and Peters (1998) specifically predict competition to be lowest in

settings with abundant tree cover, as these areas reduce carcass visibility, have low carnivore (particularly hyena) density, provide arboreal refuges for tree-climbing hominins, and offer a more diverse selection of resources. The archaeological record of lowermost Bed II appears to conform to this proposition, as artifact density and diversity are negatively correlated with levels of epiphyseal destruction, which “may indicate that hominins discarded or lost a greater quantity and variety of stone artifacts on parts of the paleolandscape where bone ravaging by hyenas was relatively low, as expected for places affording lower predation risk” (Blumenschine et al., 2012a: 385; see also Blumenschine et al., 2005, Blumenschine et al., 2007).

Resolving this matter at Olduvai (and beyond) is key, as reliable estimates of competition can help reconstruct ecology and habitats at localized (i.e., site level) scales and establish if hominins did in fact adjust their landscape use in response to carnivore activity. This study seeks to elucidate the role of carnivore avoidance in the ecology of stone tool using hominins through multivariate estimates of carcass destruction and their relation to patterns of stone tool reduction and carcass butchery during Bed I (ca. 1.9–1.8 Ma) and II (ca. 1.8–1.2 Ma) times. Because levels of bone destruction are related to the intensity of on-site competition among carnivores for access to carcass resources (see below), these data are used to determine whether, or to what extent, this parameter conditioned hominin site use in the paleo-Olduvai Basin.

2. Carnivore competition and early hominin ecology

For interspecific competition (increased predation risk is included here) to occur, two conditions must be met (Arthur, 1987: 113–116): niche overlap and resource limitation. Competition should thus be most intense within guilds, which, by definition, utilize similar resources in similar ways (Simberloff and Dayan, 1991). Field studies among modern guilds of large (here ≥ 20 kg) African carnivores document high potential niche overlap (Caro and Stoner, 2003) and frequent cases of intraguild predation (Palomares and Caro, 1999, Van Valkenburgh, 2001), both of which can result in dramatic reductions in the population sizes of inferior competitors (Creel and Creel, 1996, Trinkel and Kastberger, 2005). Given the greater diversity of the Early Pleistocene large carnivore guild (Werdelin and Lewis, 2005; although time-averaging can artificially inflate diversity in individual assemblages, see O'Regan and Reynolds, 2009) and the likelihood that past carnivore densities were higher in the absence of modern human culling (Van Valkenburgh, 2001: 114–115), interspecific competition was probably at least as intense as it is in modern African ecosystems. Indeed, several of the Bed I bone accumulations from Olduvai, now considered largely the result of carnivore (predominantly large felid) behavior, are much denser than ethologically documented feeding sites, which suggests that particularly intense competition may have required carcass transport and refuging by carnivores in frequencies not observed in modern East African savannas (Domínguez-Rodrigo et al., 2007d).

Contemporary African carnivore guilds compete for and partition shared resources along a number of axes (e.g., Mills and Biggs, 1993). However, in order for competition with carnivores to qualify as a significant factor in the adaptive responses of hominin groups, it must be shown that resource utilization intersected to some extent. This does in fact appear to be the case, as hominins and carnivores overlapped in the use of at least two key affordances: large mammal carcasses and space. Relative to most plant foods, animal carcasses are rare and exhibit short resource lives that are typically measured in days, if not hours (Blumenschine, 1986). The menu

of food items a carcass can provide to prospective consumers is regulated by a number of factors, including the condition of the carcass upon recovery (e.g., complete or partially consumed, fresh or desiccated), the ability and/or motivation of individuals or groups to monopolize access, the extractive capabilities of consumers and, in many cases, the intensity of competition (Blumenschine and Marean, 1993). Competition is itself driven by the availability of carcasses, which in turn is determined by carnivore-to-prey ratios and habitat type (Blumenschine et al., 1994). In savanna mosaic ecosystems, for example, open habitats tend to exhibit higher levels of competition because visibility is good and cues to carcass location (e.g., vultures) are common (Blumenschine, 1987, Creel and Creel, 1996, Creel and Creel, 1998, Domínguez-Rodrigo, 2001). Space is also a valuable commodity among carnivores, and subordinate species in the guild hierarchy will actively avoid those of higher rank, even if it means surrendering habitats of high prey density (Mills and Gorman, 1997, Durant, 1998, Durant, 2000, Spong, 2002).

The presence of butchery marks among Early Pleistocene faunas, nearly all of which occur on animals larger than those typically acquired by non-human primates (e.g., Bunn and Kroll, 1986, Domínguez-Rodrigo et al., 2005, Ferraro et al., 2013), demonstrates that hominins were periodically engaged in at least exploitative competition with carnivores for access to carcasses. Given the limited amount of time that most bones remain nutritionally attractive (and thus worthy of receiving the attention of either a stone tool or tooth), the not uncommon co-occurrence of butchery marks and carnivore tooth marks on the same specimens (Egeland et al., 2004) may even indicate that carcass use was closely spaced and thus reflect sporadic instances of interference competition. Similarly, the association of butchered bones and/or stone tools with tooth-marked bones reveals that hominins and carnivores overlapped in their use of space. This may have played out either in on-site competitive contests over access to carcasses (interference competition) or, probably more commonly, the independent and serial use of sites by hominins and large carnivores attracted, as Isaac (1983: 9) puts it, to “common amenities” such as water, shade, trees, or food (exploitative competition).

Having discussed the potential significance of competition between hominins and carnivores, it is important to point out that competition in general and for carcasses and space in particular would have been neither stable nor continuous. This is especially true for carcass competition in seasonal environments (Blumenschine, 1986, Blumenschine, 1987, Blumenschine et al., 1994). So, any competition or increased predation risk experienced by largely vegetarian hominins foraging within a seasonal savanna mosaic environment could probably range from intense to almost non-existent.

3. Materials and methods

Even if competition played a significant, if irregular, role in mediating hominin adaptive responses, its applicability rests on our ability to detect it taphonomically. Fortunately, a wealth of innovative studies permits such visibility to be assessed. Most of these analyses work from the premise that competition and carcass destruction covary in some systematic way; that is, as competition among carnivores for carcass resources increases, so too will the level of destruction, a process that can ultimately result in the consumption of an entire carcass, bones and all. This in turn is largely, though not exclusively, regulated by density: carnivores tend to consume and thus delete less dense bones or bone portions (e.g., vertebrae, limb epiphyses) more

often (Brain, 1967, Brain, 1969), likely because they contain more grease (Marean et al., 1992). Estimates of competition are, therefore, essentially measures of carcass destruction.

This analysis uses five indices to estimate the degree of carcass destruction: the frequency occurrence of complete major long bones, the ratio of limb bone shaft specimens to limb bone epiphyseal specimens (Blumenschine and Marean, 1993, Blumenschine et al., 1994), and the ratios of ribs and vertebrae to major long bones, femora to tibiae, and proximal humeri + distal radii to distal humeri + proximal radii (Domínguez-Rodrigo and Organista, 2007: 208–213). In each of the final four ratios, the numerator represents bones or bone portions that are less dense and thus more susceptible to deletion, while the denominator represents denser bones or bone portions (see Egeland, 2008: 23–26 for further discussion).

While all of these measures should continue to be scrutinized (e.g., Faith et al., 2007), available taphonomic data from modern African savannas support the contention that they reflect competition to some extent. Numerous observations, for example, confirm that carnivores ignore within-bone nutrients and even substantial amounts of flesh in habitats saturated with carcasses (e.g., Blumenschine, 1987: 388; Domínguez-Rodrigo and Organista, 2007: 208), a situation that results in higher frequencies of complete, undamaged bones. Complete limb bones in particular are more often encountered in closed versus open settings and, more generally, in habitats with lower carnivore (particularly spotted hyena) densities (Blumenschine, 1989, Domínguez-Rodrigo, 1996, Faith and Behrensmeyer, 2006). In hyena dens, presumably also a lower competition setting, between 17 and 35% of all limb bones are complete (Lam, 1992, Pokines and Kerbis Peterhans, 2007, Egeland et al., 2008, Prendergast and Domínguez-Rodrigo, 2008). The ratios of epiphysis to shaft fragments and ribs and vertebrae to major long bones are systematically lower in the less competitive Serengeti than the carnivore-dense, and thus highly competitive, Ngorongoro ecosystem (Blumenschine, 1989, Capaldo, 1995), and Behrensmeyer (2007) documents dramatic reductions in axial bone representation in Amboseli between 1975 and the early 2000s coincident with the expansion of open grasslands (typically high competition habitats) and swells in predator, especially spotted hyena, population sizes (see also Faith and Behrensmeyer, 2006).

This is not to say that carcass destruction is influenced solely by competition. Felids, for instance, though fully capable of eliminating parts of smaller carcasses, are known to be less efficient bone crushers than canids and hyaenids (Pobiner and Blumenschine, 2003), and the order in which various carnivores gain access to carcasses determines the range of resources available to them and, thus, what will or will not be consumed and potentially destroyed (Blumenschine and Marean, 1993, Capaldo, 1998). Although hominins can also be considered as a potential source of destruction, their role was likely limited to the fragmentation of complete limb bones and the creation of numerous shaft fragments via marrow cracking – the absence of boiling technology for grease extraction probably dampened any incentive to crush epiphyses and vertebrae intensively enough to render them either practically (i.e., made unidentifiable) or actually absent from an assemblage. Each of these factors is considered on a case-by-case basis in the interpretations that follow.

Table 1. Taphonomic and archaeological data for analyzed Bed I and II sites.^{a, b, c, d, e}

Site	Bed	Age	Complete	EP:SH	Axial:Limb	Femur:Tibia	HMPR + RDDS:HMDS + RDPR	Component loading	Artifact density (number/m ³)	Butchered bone density (number/m ³)
DK 2	I	1.86	0.07	0.22	0.34	0.78	0.46	0.0013	2.31	0.05
DK 3	I	1.86	0.09	0.15	0.27	0.82	0.23	-0.4300	13.14	0.06
FLK Zinj	I	1.84	0.12	0.19	0.52	0.71	0.20	-0.0819	90.48	8.74
FLKNN 1	I	1.84	0.14	0.87*	1.00	1.00	0.33*	0.9225	1.85	0.00
FLKNN 2	I	1.84	0.25	0.90	0.36	0.67	0.23	0.3853	0.00	0.02
FLKNN 3	I	1.84	0.40	0.37	0.42	1.25	0.55	0.8924	2.23	0.00
FLKN 1-2	I	1.82	0.14	0.46	0.35	0.58	0.40	0.2517	23.05	0.63
FLKN 3	I	1.82	0.15	0.58	0.63	0.60	0.13	0.1594	10.30	0.06
FLKN 4	I	1.82	0.10	1.29	0.35	0.90	0.22	0.1829	2.55	0.14
FLKN 5	I	1.82	0.16	0.23	0.24	0.55	0.24	-0.2331	2.51	0.02
FLKN 6	I	1.82	0.41	4.80	1.40	0.60	0.83	3.0375	6.59	0.05
FLK 15	I	1.82	0.03	0.34	0.14	0.66	0.18	-0.8130	0.13	0.00
HWKE 1-2	II	1.76	0.03*	1.70	0.71	0.70*	0.18*	0.3563	2.90	0.04
HWKE 3-5	II	1.6	0.03	1.60	0.50	0.38	0.18*	0.1311	19.83	0.00
MNK Main	II	1.4	0.11	0.21	0.51	0.81	0.18*	-0.1404	42.79	0.03
FCW	II	1.4	0.00	0.23	0.33	1.00	0.25	-0.7372	253.16	0.00
TK UF	II	1.2	0.00	0.13	0.08	1.33	0.00	-2.1029	720.69	0.00
TK LF	II	1.2	0.00	0.14	0.14	0.00	0.18*	-1.2319	558.94	0.00
BK	II	1.2	0.04	0.15	0.23	0.87	0.29	-0.5493	42.22	0.29
BK 4b	II	1.2	0.02	0.59*	0.77	0.50	0.18*	-0.0008	30.72	5.22

^a Taphonomic variables and butchered bone counts derive from data in the following sources: DK 2, 3: Egeland (2007c: Table 81, 82, 83, 84, 85, 86); FLK Zinj: Bunn (1986: Table 4), Bunn and Kroll (1986: Table 4), Domínguez-Rodrigo and Barba (2007a: Table 16; 2007b: Table 2 and 3); FLKNN 1: Barba and Domínguez-Rodrigo (2007: Table 62, 63); FLKNN 2: Bunn (1982: 139), Egeland (2007b: Table 69, 70, 72, 73); FLKNN 3: Domínguez-Rodrigo and Barba (2007d: 245, Table 75, 76, 77), Egeland (2008: Table 3); FLKN 1-2: Bunn (1986: Table 2), Domínguez-Rodrigo and Barba (2007c: 134, Table 32, 36); FLKN 3, 4: Domínguez-Rodrigo et al. (2007c: 176, 177, Table 42, 43, 44, 46), Egeland (2008: Table 3); FLKN 5: Egeland (2007a: 193, Table 50, 51, 53, 54); FLKN 6: Bunn et al. (2010: 361), Domínguez-Rodrigo et al. (2007a: Table 18, 19), Egeland (2008: Table 3), FLK 15: Domínguez-Rodrigo and Organista (2007: Table 57), Egeland (2008: Table 3); HWKE 1-2: Egeland (2008: Table 3), Monahan (1996a: Table 5); HWKE 3-5, MNK Main, FCW, TK UF, TK LF, BK: Egeland and Domínguez-Rodrigo (2008: 1040, Table 3, 9, 10); BK 4b: Domínguez-Rodrigo et al. (2014).

^b Artifact counts derive from data in the following sources: DK 2, 3, FLK Zinj, FLKN 1-2, 3, 4, 5, 6, FCW, TK UF, TK LF: de la Torre and Mora (2005: Table 9.4), FLKNN 1: Leakey (1971: 47); FLKNN 3: Domínguez-Rodrigo and Barba (2007d: 247); FLK 15: Domínguez-Rodrigo and Organista (2007: 215); HWKE 1-2, 3-5, MNK Main, BK: Monahan (1996a: Table 1); BK 4b: Díez-Martín et al. (2009: Table 1).

^c Artifact and butchered bone densities calculated based on excavation area and depth estimates in the following sources: DK 2, 3: Potts (1988: 333); FLK Zinj: Leakey (1971: 49); FLKNN 1: Leakey (1971: 40); FLKNN 2: Potts (1988: 361); FLKNN 3: Potts (1988: 351); FLKN 1-2: Kroll (1994: 113); FLKN 3, 4, 5: Kroll and Isaac (1984: Table 3); FLKN 6: Potts (1988: 381); FLK 15: Leakey (1971: Fig. 23); HWKE 1-2, 3-5, MNK Main, BK: Monahan (1996a: Table 1); FCW: Leakey (1971: 156); TK UF: Petraglia and Potts (1994: Table 1); TK LF: Leakey (1971: 172); BK 4b: Domínguez-Rodrigo et al. (2014).

^d Values marked with an asterisk (*) are not directly calculated but represent the mean Bed I or Bed II value.

^e Abbreviations: EP = epiphyseal fragment; SH = shaft fragment; HM = humerus; RD = radius; PR = proximal; DS = distal.

The occurrence of complete long bones is calculated as the number of complete bones divided by the Minimum Number of Elements (MNE) for all major long bones (humerus, radius, metacarpal, femur, tibia, metatarsal) combined, while epiphysis-to-shaft ratios are derived from the Number of Identified Specimens (NISP) from each category that are green-broken (complete bones are not considered), thus ignoring those fragments generated diagenetically. The ribs and vertebrae to major long bones, femora to tibiae, and proximal humeri + distal radii to distal humeri + proximal radii ratios are based on MNE counts, the calculation of which include midshaft fragments. All data represent combined values for Size Class 1–4 carcasses (Size Classes follow Brain, 1974, Bunn, 1982). While a majority of these data are available for the faunal assemblages, there are a handful of instances where a ratio cannot be calculated, in which case the mean Bed I or Bed II value is assigned (these are identified in Table 1). Several models of competition have been proposed based on these and other variables (e.g., Haynes, 1982, Blumenschine and Marean, 1993, Blumenschine et al., 1994, Monahan, 1996a, Faith and Behrensmeier, 2006, Domínguez-Rodrigo and Organista, 2007, Faith et al., 2007, Egeland, 2008), and here I expand on these studies by integrating the five above-mentioned measures into a multivariate (cf. Binford, 1981: 262–278) principal component analysis (PCA).

Lithic discard rates are used as a proxy for occupation intensity and are estimated by the number of artifacts per m³. While artifact weight densities are preferable because they better control for differences in reduction intensity across sites, these data are currently unavailable for several of the sites considered here. The level of hominin involvement with carcasses is estimated through the number of butchered bones per m³. Here, a “butchered” bone is any specimen preserving cutmarks and/or percussion marks (i.e., pits with microstriations and/or fields of microstriations; Blumenschine and Selvaggio, 1988, Pickering and Egeland, 2006). The effects of sedimentation rates, recovery methods, and level of site disturbance on estimates of find densities are considered in detail below.

3.1. The study sites

Olduvai Gorge is located in northern Tanzania between the western margin of the East African Rift and the eastern edge of the Serengeti Plain (Fig. 1). The basin itself developed about 2.0 Ma and the modern gorge formed over the course of the Middle and Late Pleistocene through tectonically induced fluvial incision. Metamorphic basement rocks underlie the basin, and those such as Naibor Soit and Kelogi that outcrop today as inselbergs probably served as important sources of lithic raw material throughout the Early Pleistocene (Hay, 1976). Of the modern gorge's 100 m-thick sedimentary record, the lowermost geological units, Beds I and II, are of most concern here. The stratigraphy of the reworked volcanoclastic sediments and airfall tuffs that make up Beds I and II are well documented through field mapping, paleomagnetism, tephra correlation, and K/Ar and ⁴⁰Ar/³⁹Ar dating, all of which place the deposition of these units between ca. 1.9 and 1.2 Ma (Hay, 1976, Manega, 1993, Blumenschine et al., 2003, McHenry, 2012).

During Bed I and lower Bed II times Olduvai was a shallow, hydrologically closed basin that contained a saline and alkaline playa lake of fluctuating size (Hay, 1976, Hay and Kyser, 2001, Ashley and Hay, 2002). The basin's eastern margin was dominated by an extensive alluvial fan formed by sediments transported down from the volcanic highlands to the south and east of

the lake (Fig. 2). All of the Bed I archaeological occurrences considered here occur in what Hay (1976) termed the Eastern Lake Margin lithofacies. The lake expanded and contracted several times until, during Upper Bed II times (after about 1.3 Ma), the perennial lake disappeared and was eventually replaced by fluvial systems.

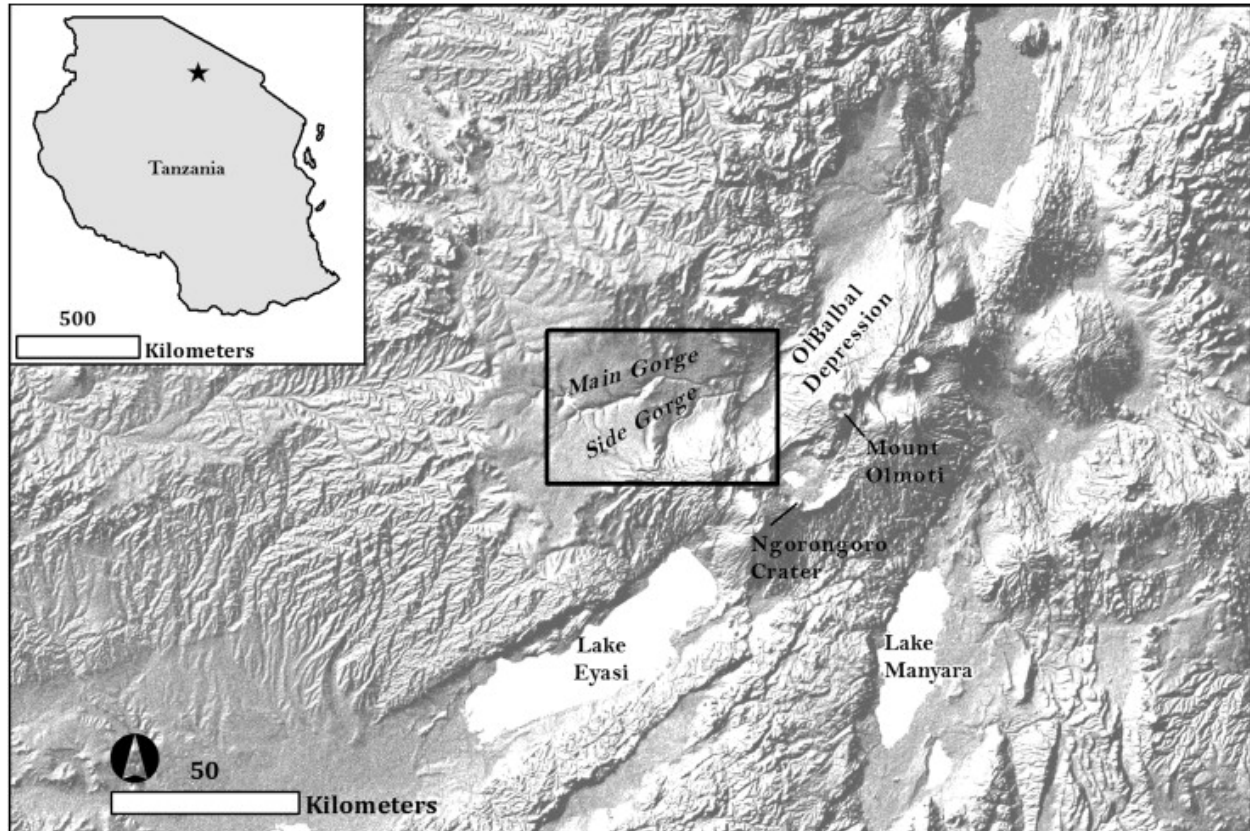


Fig. 1. Location of Olduvai Gorge and other significant landforms.

The Bed I assemblages included in the analysis are DK Levels 2 and 3 [DK 2 and 3], FLK Level 22 *Zinjanthropus* [FLK Zinj], FLK North Levels 1–2, 3, 4, 5, and 6 [FLKN], FLK North North Levels 1, 2, and 3 [FLKNN], and FLK Level 15 [FLK 15], while those from Bed II derive from HWE East Levels 1–2 and 3–5 [HWKE], MNK Main, FC West Floor [FCW], TK Upper Floor [TK UF], TK Lower Floor [TK LF], BK, and BK Level 4b [BK 4b]; all but one of these (BK 4b; Domínguez-Rodrigo et al., 2009b, Domínguez-Rodrigo et al., 2014) are based on analyses of Mary Leakey's (1971) excavations from the 1960s (Domínguez-Rodrigo et al., 2007b, Egeland and Domínguez-Rodrigo, 2008).

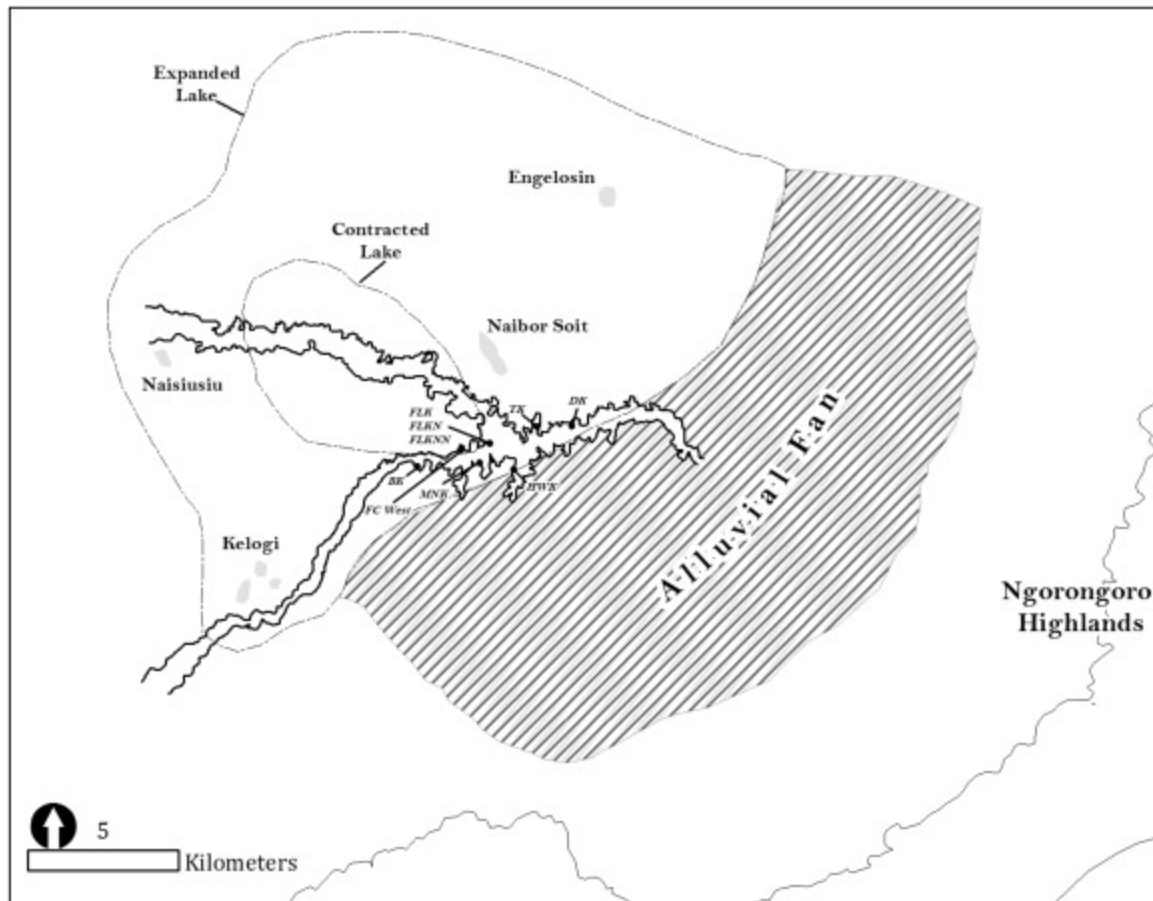


Fig. 2. Paleogeographic reconstructions of the paleo-Olduvai basin during Bed I times and the location of the study sites. Modified from Hay (1976: Fig. 18) and Ashley et al. (2010a: Fig. 1).

Although it is not known whether sedimentation rates varied between sites, considerable differences are not expected within the paleo-Olduvai Basin's low gradient lake margins; indeed, most analyses assume a constant, and relatively low, rate throughout the gorge (Kappelman, 1984, Hay and Kyser, 2001, Ashley, 2007). Leakey (1971: 42, 49, 62, 118) states that screening was carried out at FLKNN, FLK Zinj, FLKN, and MNK Main, and screen bags with small (<4 cm) finds that lack catalogue numbers exist within these collections along with that of DK (personal observations; M. Domínguez-Rodrigo, personal communication). It is possible, however, that with the exception of FLK Zinj these sites were not screened systematically or, perhaps, that some material was not retained or was subsequently lost, as recent excavations at FLKN (Bunn et al., 2010) and DK (work in progress) have uncovered screened material at higher rates than are observed among Leakey's original collections. Potts (1982: 62) notes that the DK sediments were generally screened only when finds were densely concentrated as they were, for example, at the base of Level 3. As for the remaining sites (FLK 15, HWKE, FCW, TK, BK), Leakey (1971) does not comment on the use of screens, although Petraglia and Potts (1994: 239) and Kimura (1999: 811) report that screening was conducted at FCW, TK UF, and HWKE. This contention is supported at least for the former sites by de la Torre and Mora's (2005: 118, 138, 140) finding that fragments <2 cm make up a significant portion of the TK (both UF and LF) and FCW lithic assemblages. The BK 4b sediments were systematically screened, although this may not have been the case for the 1963 BK excavations.

There is general agreement that very little material was removed from the FLK sites after their original deposition (Potts, 1988, Petraglia and Potts, 1994, Domínguez-Rodrigo et al., 2012). The common occurrence of small gravels and pebbles within the DK silts suggests some level of fluvial activity, perhaps as sheetwash (Hay, 1976: 48), although this process likely resulted in the transport of allochthonous materials to the site rather than the removal of finds from the deposited assemblage (Potts, 1988: 58–59). FCW, HWKE and, to a lesser extent, TK UF and MNK Main, appear to have experienced some winnowing of the smallest pieces (Petraglia and Potts, 1994, Kimura, 1999, Egeland and Domínguez-Rodrigo, 2008). Rounded bone fragments and lithics are present in Leakey's BK collection, although a vast majority of the fauna is in excellent condition and small debitage is also quite common (Leakey, 1971, Monahan, 1996a). To the extent that data from BK 4b can be applied to the site as a whole, the fluvial deposits that characterize the area were active enough only to remove materials <2 cm (Domínguez-Rodrigo et al., 2014). To summarize: the reported find densities at FLK Zinj and BK 4b are likely very close to what was originally deposited; those for the remaining assemblages are probably slightly underestimated due to a combination of recovery bias and either curatorial loss or post-depositional removal of materials.

4. Results

Measures of carcass destruction and artifact and butchered bone densities are listed in Table 1 for the Olduvai assemblages. There is no evidence for a non-linear relationship between any of the carcass destruction variables, but they are all somewhat right-skewed, so a square-root transformation was performed prior to the PCA in order to better approximate normal distributions. An exploratory PCA with all five transformed measures reveals that the femur-to-tibia ratio is only weakly correlated with the others, which implies that it does not in fact measure the same underlying factor (i.e., carcass destruction). Discarding this variable produces a matrix of moderate to high correlations (Table 2) and a single component solution that explains nearly 67% of the total sample variance. Because the component loadings (see Table 1) for each assemblage condense these four variables into a single dimension, higher scores (e.g., FLKN 6) can be interpreted to reflect lower overall levels of carcass destruction and, therefore, modest levels of inferred competition among carnivores for carcass resources, while lower scores (e.g., TK UF) represent higher degrees of competition.

Table 2. Correlation matrix for principal component analysis.^a

Variable	Complete	EP:SH	Axial:Limb	HMPR + RDDS:HMDS + RDPR
Complete	1.00			
EP:SH	0.43	1.00		
Axial:Limb	0.52	0.74	1.00	
HMPR + RDDS:HMDS + RDPR	0.67	0.45	0.53	1.00

^a Abbreviations: EP = epiphyseal fragment; SH = shaft fragment; HM = humerus; RD = radius; PR = proximal; DS = distal.

Fig. 3 shows that the Olduvai faunas vary along a continuum of carcass destruction levels. FLKN 6 is by far the least ravaged and, in fact, appears as somewhat of an outlier in this context. Among the other Bed I assemblages, the three levels at FLKNN cluster together within a presumed lower competition setting, while the FLKN faunas, along with DK 2, show moderate

levels of carcass destruction. DK 3, which Leakey (1971: 258) identifies as the oldest of the Olduvai living floors, along with FLK 15 fall in the area of relatively intense carnivore ravaging. Other than HWKE 1–2, all the Bed II assemblages show a moderate to high degree of bone destruction. I argued previously, based on a bivariate analysis, that carcass destruction was more intense among the Bed II assemblages relative to those from Bed I (Egeland, 2008) and, comparing the multivariate-based component loadings between the two time periods, Bed II does in fact display lower scores (= higher levels of carcass destruction), and this difference is statistically significant at the 0.05 level (two-tailed Mann–Whitney U test: $U = 22$, $Z = -2.006$, $p = 0.045$; two-tailed t -test: $t = 2.214$, $p = 0.048$).

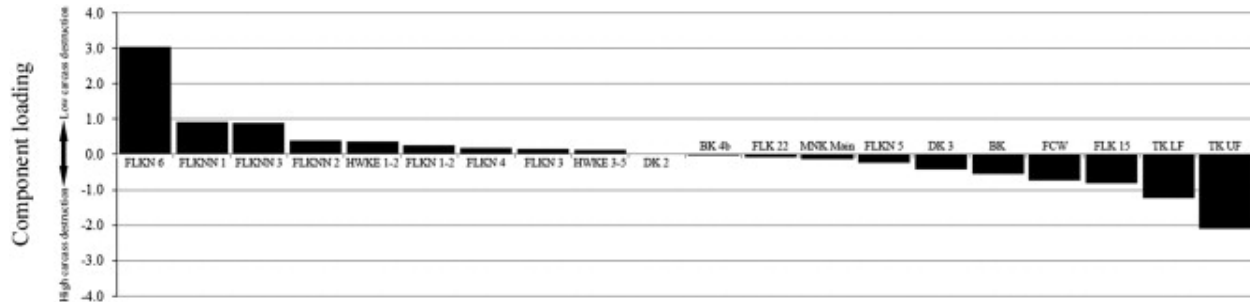


Fig. 3. Histogram of component loadings for Olduvai sites.

Artifact densities for the combined Bed I and II sample show a significant positive correlation with carcass destruction; that is, as levels of carcass destruction increase (= lower component loadings) so too does the frequency of lithic debris ($r = 0.638$, $p = 0.002$; $r_s = 0.585$, $p = 0.007$), which, it should be recalled, is probably underestimated for most of the assemblages. The removal of FLKN 6, FCW, and TK from the analysis results in a statistically insignificant relationship ($r = 0.293$, $p = 0.272$; $r_s = 0.421$, $p = 0.105$), which suggests that the correlation between lithic discard and carcass destruction is largely driven by these outlier assemblages. No relationship exists among the Bed I assemblages ($r = 0.137$, $p = 0.671$; $r_s = 0.175$, $p = 0.587$) and, for the Bed II assemblages, the relationship between carcass destruction and lithic density for all the sites is positive and highly significant ($r = 0.950$, $p = 0.000$; $r_s = 0.976$, $p = 0.000$), a pattern that holds even when the FCW and TK assemblages are excluded ($r = 0.880$, $p = 0.049$; $r_s = 0.900$, $p = 0.037$). The density of butchered bones among the Bed I and II sites, again likely underestimated in most cases, exhibits no relationship with estimates of competition ($r = 0.135$, $p = 0.605$; $r_s = 0.334$, $p = 0.190$). No association exists between these variables when the Bed I ($r = 0.149$, $p = 0.645$; $r_s = 0.336$, $p = 0.286$) and Bed II ($r = 0.024$, $p = 0.970$; $r_s = 0.300$, $p = 0.624$) assemblages are considered separately.¹

5. Discussion

Based on multivariate estimates of carcass destruction, there is evidence to suggest that hominins throughout Bed I and II times actually focused more intensive tool reduction behavior at sites with *higher* levels of inferred carnivore competition, although this pattern appears to be heavily influenced by the extremely low levels of bone destruction at FLKN 6 and the large lithic

¹ The FC West and TK faunal assemblages are not included in the analysis as the lack of butchery marks at these sites is most likely an artifact of extremely poor cortical surface preservation (Monahan, 1996b; Egeland and Domínguez-Rodrigo, 2008).

assemblages from FCW and TK, both of which exhibit intense ravaging. There is no systematic relationship between lithic reduction and competition over the ca. 650,000 years sampled by the remaining Bed I and II sites. This latter configuration holds among the Bed I sites when considered on their own, but, interestingly, there is a very strong tendency among hominin populations throughout Bed II times to more thoroughly carry out tool production in areas that probably experienced relatively high levels of carnivore competition and predation risk.

No association can be detected between the intensity of hominin butchery behavior and levels of competition during either Bed I or II times. This is not entirely surprising given the lack of variability in butchery mark frequencies—there are, after all, only two faunal assemblages, those from FLK Zinj and BK, that are largely anthropogenic, while at the remaining Olduvai sites, butchery marks, and thus hominin involvement with carcasses, is uniformly rare (Domínguez-Rodrigo et al., 2007b, 2014; Egeland, 2008, Egeland and Domínguez-Rodrigo, 2008). Ongoing excavations may change this, as definitive signs of butchery have been reported from recently uncovered faunal material from TK (J. Yravedra, personal communication).

Two propositions flow from these findings. The first is that variability in hominin habitat selection and occupation intensity during Bed I times, at least as reflected by the number of artifacts discarded at sites, does not appear to have been regulated by carnivore avoidance. Still, it must be kept in mind that all but two of the Bed I assemblages analyzed here (DK 2 and 3 being the exceptions) derive from only three locales (FLK, FLKN, and FLKNN), all of which cluster near the gorge's junction within an area less than 0.05 km². While temporal and spatial variability in habitats certainly existed between and among these locations (Cerling and Hay, 1986, Plummer and Bishop, 1994, Sikes, 1994, Barboni et al., 2010), they sample only a small, and undoubtedly biased, fraction of Bed I paleolandscapes. There may simply not yet be enough variability to explain, and continued excavations of the FLK Zinj land surface in particular will no doubt alleviate this bias (Domínguez-Rodrigo et al., 2010, Blumenschine et al., 2012b). Regardless, that this circumscribed area is so densely packed with lithic and faunal material strongly suggests the presence of specific landscape features that attracted both hominins and large carnivores over tens of thousands of years. Probably the most important of these were groundwater-fed springs at FLKNN and FLKN, both of which provided the only documented sources of fresh water in the entire area. The springs supported wooded to densely wooded habitats during middle Bed I times at both FLKNN and FLK Zinj (Ashley et al., 2010b) and, during upper Bed I times, a groundwater forest situated within a more open wooded grassland at FLKN (Bamford et al., 2008, Barboni et al., 2010, Ashley et al., 2010a). A closed, and thus lower competition, habitat is also supported at FLKNN by the modest carcass destruction documented in its faunal assemblages, while slightly elevated, though not intense, levels of inferred competition among the FLKN collections (save perhaps for FLKN 5) are consistent with the drier and slightly more open environments of upper Bed I (Kappelman, 1986, Fernández-Jalvo et al., 1998, Hay and Kyser, 2001, Sikes and Ashley, 2007). Large felids appear to have been particularly active carcass accumulators at FLKN and FLKNN (Domínguez-Rodrigo et al., 2007b), a finding that, along with a low competition setting that experienced only sporadic hyena involvement, also helps explain the lower levels of damage among most of these bone assemblages. The other significant factor conditioning stone and bone accumulation at the junction sites is the presence of well-drained, topographic highs at both FLKN and FLK Zinj where slight differences in local relief provided dry, useable land amid nearby wetlands (Ashley

et al., 2010a, Ashley et al., 2010b, Blumenschine et al., 2012b). These locally unique combinations of landscape facets thus attracted a variety of animals, including hominins, to the vicinity in search of assorted resources.

While it may be that other factors played a more proximate role in determining the location of hominin archaeological activities, it is probably premature to assert that carnivore avoidance and competition played no role whatsoever in the daily routines of Bed I hominins. After all, many of the lithic assemblages are associated with lower levels of carcass destruction (Fig. 3). Returning to FLK Zinj, for example, there is now general agreement that fresh water and tree cover played a role in drawing hominins to the site and, further, that the bone assemblage represents in part the remains of carcasses transported primarily from the edge of a nearby water source (Domínguez-Rodrigo et al., 2010, Blumenschine et al., 2012b). Blumenschine et al. (2012b) consider the FLK Zinj fauna to reflect a mixture of carcasses deposited directly by carnivores and carcasses scavenged by hominins from abandoned felid meals acquired either directly on-site or transported from nearby kills, all of which were subsequently ravaged by bone-crushing carnivores. While they concede that the wooded habitat of FLK Zinj would have allayed predation risk, Blumenschine et al. (2012b) argue that relatively high rates of tooth-marking and epiphyseal destruction and the remnants of three hominin individuals, possibly the victims of predation, indicate that carnivores were quite active in the neighborhood, implying that hominin site use was ephemeral and limited to feeding.

Domínguez-Rodrigo et al. (2010), on the other hand, argue convincingly that the FLK Zinj fauna is largely anthropogenic, with carnivores relegated mainly to marginal scavenging of bone refuse. The site itself is regarded as low competition with little associated predation risk, whereas the inferred location of carcass acquisition, the edge of the FLKNN spring approximately 200 m to the north, would, as a source of permanent water, draw predators on the lookout for hapless prey. Carnivore activity is reconstructed to be low across the Level 22 land surface, not only at FLK Zinj itself, but at the coeval FLKNN 1 spring. Accordingly, “when hominins created the cluster at FLK Zinj, carnivores were not as active around the spring as in earlier times. Further... when hominins created FLK Zinj, they did so by choosing a spot where carnivore activity was minimal, away from the spring area where carnivore risk may have been higher, at a time when carnivores were relatively inactive around the spring” (Domínguez-Rodrigo et al., 2010: 328).

If FLK Zinj was indeed chosen because of its low carnivore activity, levels of on-site carcass destruction should be lower than those of the surrounding area, including the adjacent spring at FLKNN 1. While inferred competition at FLKNN 1 is actually lower (Fig. 3), there are good reasons to suspect that carcass destruction at FLK Zinj is overestimated, with hominin behavior a major cause. Table 1 shows that intense axial and especially epiphyseal destruction are responsible for the high level of estimated carnivore ravaging at FLK Zinj. The frequency and anatomical placement of cutmarks and percussion marks demonstrate that in many cases hominins enjoyed unfettered access to meat and marrow from fully fleshed carcasses (Blumenschine, 1995, Domínguez-Rodrigo and Barba, 2007a, Domínguez-Rodrigo and Barba, 2007b), leaving carnivores little to consume but nutrient-poor limb bone shaft fragments, a few unbroken bones, and the grease from axial parts and limb bone epiphyses. Couple this limited menu with the fact that hammerstone breakage produces disproportionate numbers of shaft fragments (Bunn, 1989, Pickering and Egeland, 2006), and epiphyseal representation is further

depressed. What is more, Domínguez-Rodrigo et al. (2010) estimate based on actualistic data that axial bone loss at FLK Zinj is greater than predicted by the site's low frequencies of tooth-marked epiphyses (<30%). The dearth of axial bones, they argue further, is thus best explained by a mixed strategy of hominin carcass transport rather than carnivore ravaging: “[t]he extreme paucity of ungulate axial elements at the site is probably not related to post-hominid, carnivore destruction of select parts of whole skeletons, but rather to selective transport of long limb bones from carcasses by hominids...[t]he presence, though, of some axial elements in the assemblage indicates that hominids did transport some carcasses to the site in a complete or nearly complete state, which carnivores may have subsequently ravaged” (Domínguez-Rodrigo et al., 2010: 331). If this scenario is correct, then bone destruction at FLK Zinj is lower than the taphonomic measures in Table 1 indicate, and perhaps the intensive utilization of the site by hominins was in fact due, at least in part, to the safety it furnished. This leaves open the possibility that the occupation of FLK Zinj involved activities beyond simply feeding (Isaac, 1978, Rose and Marshall, 1996).

If artifact density is any indication, the other Bed I localities appear to have been only sporadically used by hominins and, with the exception of a handful of butchered bones from each assemblage, these visitations were largely unrelated to carcass butchery (Domínguez-Rodrigo et al., 2007b). At FLKN and FLKNN, stone tool use was geared principally towards battering and pounding, probably of plant foods, rather than the production of sharp-edged stone knives (de la Torre and Mora, 2005, Díez-Martín et al., 2010, Blumenshine et al., 2012b). Site use by hominins and carnivores was in most cases serial and unrelated, with interactions limited to exploitative competition for wooded sanctuaries. While the paleoecology of DK is known with less precision than that of the junction sites, it does offer an interesting contrast in terms of its paleogeographic setting, moderate to intense levels of carcass ravaging, and, unlike FLKN and FLKNN, fair amount of flaking debris. The hominin contribution to the DK bone assemblages is marginal (a total of only 14 butchered bones occur in the combined DK 2 and 3 sample; Egeland, 2007c) but, if the numerous flakes present within the lithic collection (de la Torre and Mora, 2005) are considered to be butchering tools, as experiments with and use-wear of Oldowan flakes suggest (Jones, 1981, Jones, 1994, Keeley and Toth, 1981, Schick and Toth, 1993), perhaps hominin carcass processing focused on the skinning and/or disarticulation of parts subsequently transported away from what, according to this analysis, was a particularly active and, in contrast to what I argued previously (Egeland, 2007c: 263), competitive predation arena. The hominin signal at the site may, in other words, be minor precisely because a desire to minimize potential carnivore encounters encouraged the removal of hastily butchered carcass parts elsewhere. Ongoing excavations in the DK area are focused on evaluating this hypothesis.

The second major finding is that by at least upper middle Bed II times (after ca. 1.4 Ma) hominins were able to establish control of, and carry out a variety of tool-making activities within, highly competitive habitats like those evinced at FCW, BK, and TK (Monahan, 1996a, Egeland, 2008, Egeland and Domínguez-Rodrigo, 2008). Certainly at BK, and possibly at FCW and TK, hominins thoroughly butchered several fully fleshed carcasses with little apparent concern for resident carnivores. Whether this evidently superior competitive ability was due to increases in body size, group size, and/or other behavioral developments (e.g., fire, spears) is not yet clear. Regardless, if modern ecosystems are any indication, the association of hominin behavior during Bed II times with higher competition settings may signal a shift in habitat

preferences away from wooded and towards more open environments. Alternatively, this might reflect less a preference for open habitats per se than a successful adaptive response by hominins to the drier and more open settings that increasingly characterized the Olduvai Basin after 1.5 Ma or so (Cerling and Hay, 1986, Kappelman, 1986, Sikes, 1994, Sikes, 1999). It is interesting to note that this pattern of hominin site use and habitat association roughly coincides with the disappearance of the large felid genera *Megantereon* and *Homotherium* from eastern Africa (Werdelin and Lewis, 2005), which means that hominins confronted a less diverse large carnivore guild during Bed II times. Perhaps the vacancies within the guild hierarchy produced by these extinctions permitted hominins to more readily exploit a wider variety of habitats within the Olduvai Basin. An intriguing alternative proposes that increasingly effective meat-eating by hominins was actually the cause, rather than the result, of the eventual reduction in carnivore (particularly hypercarnivore) diversity during this period (Werdelin and Lewis, 2013). Given the mounting evidence for the importance after 1.5 Ma of meat in the diets of what were probably larger, more encephalized, and permanently terrestrial hominin populations (Monahan, 1996a, Domínguez-Rodrigo et al., 2002, Domínguez-Rodrigo et al., 2009a, Domínguez-Rodrigo et al., 2009b, 2014; Pickering et al., 2004, Egeland and Domínguez-Rodrigo, 2008, Pobiner et al., 2008, Pante, 2013), this latter possibility should be taken seriously.

6. Conclusions

The tool-assisted consumption of large mammals posed novel challenges to Early Pleistocene hominin groups, not the least of which was higher encounter rates with large carnivores, and not only as prey, but as potential competitors for space and carcasses. Researchers therefore logically presume that a desire on the part of hominins to regulate the frequency and nature of those interactions determined to some extent their archaeologically visible behaviors. Levels of carcass destruction offer one means to estimate the degree of competition and, thus, evaluate the importance of carnivore avoidance in hominins' daily routines. Multivariate assessments of carcass destruction from a number of Bed I and II faunal assemblages from Olduvai Gorge range from extremely light to very intense although, in general, inferred levels of competition are higher among the latter sites. Competition does not appear to explain variability in site occupation intensity (as measured by the density of artifacts and butchered bones) other than for the Bed II subsample, in which case lithic discard is greater in areas of higher inferred competition. The overall impression is that, while carnivore avoidance may have played some part in site use and location, its effect was intermittent, and other affordances such as water, trees, dry land, food (plant and animal), and perhaps toolstone played more proximate roles, at least for the assemblages considered here (cf. Blumenschine et al., 2005: 185). Domínguez-Rodrigo et al. (2010: 327) point out that most of the Bed I hominin fossils derive from the wooded contexts of the gorge's junction sites, which, they maintain, makes some sense if arboreality was a significant component of the locomotor adaptation of *Homo habilis* (the presumed stone tool maker during Bed I times). Perhaps, then, Bed I hominins were more likely to use and discard archaeological material in wooded habitats simply because they were partially tethered to trees.

This also underscores another potential shortcoming of this study—namely its focus on sites to the near exclusion of the surrounding landscapes in which they were situated (FLK 15 is the only non-“site” assemblage included in this study). This emphasis, though necessary given the

availability of taphonomic data, makes it difficult to compare levels of competition at locales with dense accumulations of lithics and fauna (“sites”) with those areas less intensively utilized. It is therefore problematic to fully evaluate, for instance, whether or not hominins regularly surrendered more open, competitive habitats to carnivores in preference for what appear to be wooded refugia at the FLK, FLKN, and FLKNN localities during Bed I times. Similarly, it cannot currently be determined if BK, TK, and FCW, though situated within higher competition settings than their Bed I counterparts, were in fact relatively safe havens within extremely competitive Bed II landscapes. In other words, a comprehensive assessment of hominin land use requires an appreciation not only for why particular areas *were* used, but why others *were not*. The integration of so-called “background” bone scatters (e.g., Domínguez-Rodrigo and Organista, 2007) and landscape-scale taphonomy (e.g., Domínguez-Rodrigo et al., 2009a) holds great promise in this context. Blumenschine et al., 2005, Blumenschine et al., 2007, Blumenschine et al., 2012a use of epiphysis-to-shaft ratios across the paleosurfaces of lowermost Bed II hints at the potential of this perspective, although a single index, as they readily acknowledge (2005: 185), may only partially reflect competition levels. Studies of the important FLK Zinj land surface are also a move in the right direction although, unfortunately, the analyses result in some disagreement over the level of carnivore activity across the Zinj landscape relative to the site itself (compare Blumenschine et al., 2012b, Domínguez-Rodrigo et al., 2010; see discussion above). Nevertheless, it is becoming increasingly clear that the hominin populations within the Early Pleistocene Olduvai Basin performed a wide array of archaeologically visible behaviors, created an assortment of site “types,” and modified their pattern of landscape use in relation to a variety of ecological parameters.

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