Oliver, JS, Plummer, TW, Hertel, F and Bishop, LC

Bovid mortality patterns from Kanjera South, Homa Peninsula, Kenya and FLK-Zinj, Olduvai Gorge, Tanzania: Evidence for habitat mediated variability in Oldowan hominin hunting and scavenging behavior

http://researchonline.ljmu.ac.uk/id/eprint/10581/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Oliver, JS, Plummer, TW, Hertel, F and Bishop, LC (2019) Bovid mortality patterns from Kanjera South, Homa Peninsula, Kenya and FLK-Zinj, Olduvai Gorge, Tanzania: Evidence for habitat mediated variability in Oldowan hominin hunting and scavenging behavior. Journal of Human Evolution.

Bovid mortality patterns from Kanjera South, Homa Peninsula, Kenya and FLK-Zinj, Olduvai Gorge, Tanzania: Evidence for habitat mediated variability in Oldowan hominin hunting and scavenging behavior

James S. Oliver [a], Thomas W. Plummer [b], Fritz Hertel [c], Laura C. Bishop [d]

[a] *Earth and Mineral Sciences Museum, Department of Geosciences, Pennsylvania State University, 207 Deike Building, University Park, PA 16802, USA*

[b] *Department of Anthropology, Queens College, CUNY, the CUNY Graduate Center, and NYCEP, 65-30 Kissena Blvd, Flushing, NY 11367, USA*[c] *Department of Biology, California State University, 18111 Nordhoff Street, Northridge, CA 91330, USA*

[d] *The Sino British College, University of Shanghai for Science and Technology, 1195 Middle Fuxing Road, Shanghai 20031, P.R. China* and *Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool, L3 3AF, UK*

* Corresponding author.

E-mail address: joliver@museum.state.il.us (J.S. Oliver).

Keywords: Oldowan; Kanjera; FLK-Zinj; Bovid mortality; Hunting; Scavenging

Abstract

The archaeological record documents Oldowan hominin occupation of habitats ranging from open grasslands to riparian forest by 2.0 Ma. Despite this we have a poor understanding of whether hominin foraging behavior varies in different environmental settings. We compare bovid mortality profiles from the two largest Oldowan zooarchaeological samples, one from a grassland (Excavation 1, Kanjera South, Kenya) and another from a woodland (FLK Zinj, Olduvai Gorge, Tanzania) with bovid mortality samples created by African carnivores in different habitats. Kanjera hominins frequently had early access, likely through hunting, to small (size 1 = <23 kg and size 2 = 24–112 kg) juvenile bovids, creating a mortality pattern similar to that created by grassland dwelling carnivores. Kanjera hominins had more mixed access to large (size 3 = 113–340 kg), often juvenile bovids, and frequently scavenged heads. In contrast, previous work has shown that the few small bovids at FLK-Zinj were predominantly older individuals. Prime adults dominate the FLK-Zinj large bovid sample, leading to a mortality pattern similar to that created by carnivores occupying more closed habitats. Variation in bovid body size and mortality profiles between these archaeological assemblages may reflect the challenges of acquiring fauna in open versus closed habitats with a simple hunting toolkit. The heterogeneous woodland habitat of FLK-Zinj would have provided more opportunities to ambush prey, whereas on grasslands with more limited concealment opportunities Kanjera hominins focused their efforts on vulnerable juvenile prey, some likely acquired after short chases.

1. Introduction

The archaeological and paleoecological records in eastern and southern Africa show that by 2.0 Ma hominins making Oldowan tools occupied habitats ranging from open grassland to riparian forest (Plummer, 2004; Plummer et al., 2009a, b; Braun et al., 2010). Of the activities documented in these habitats one of the most significant was hominin entry into the carnivore guild about 2.6–1.8 Ma (Brantingham, 1998; Plummer, 2004). How hominins acquired carcasses—via passive scavenging, aggressive scavenging, or hunting—and how their foraging behavior varied with habitat is critical to issues ranging from hominin brain and body enlargement, cognitive abilities, and dietary evolution, to range expansion and migration out of Africa (e.g., Aiello and Wheeler, 1995; Foley, 2001; Aeillo and Wells, 2002; Lordkipanidze et al., 2013; Zhu et al., 2018).

Here we restrict detailed discussions of Oldowan hominin carcass acquisition behavior to just two sites with the largest zooarchaeological assemblages, Kanjera South, Kenya, which formed in an open grassland (Plummer et al., 2009a, b; Ditchfield et al., 2018), and FLK-Zinj, Tanzania, which accumulated in a woodland (Plummer and Bishop, 1994; Sikes, 1994; Ashley et al., 2010a, b; Blumenschine et al., 2012; Magill et al., 2016). Because multiple hominin species existed in the Plio-Pleistocene, and it is currently not possible to know the identity of the taxon or taxa making the Kanjera and FLK-Zinj assemblages, we use the term ‘Oldowan hominin’ here. This common heuristic device is used to discuss behaviors carried out at Oldowan sites without reference to a specific hominin taxon (see Plummer, 2004; Toth and Schick, 2006; Braun et al., 2008, Grine and Fleagle, 2009, Plummer et al., 2009a, Blumenschine et al., 2012, Ferraro et al., 2013). Taphonomic and zooarchaeological analyses of these assemblages have found that Oldowan hominins frequently had early access to meat-rich carcasses, and although scavenging occurred, hominins likely acquired many animals through hunting (e.g., Bunn and Kroll, 1986; Domínguez-Rodrigo and Barba, 2006, 2007; Ferraro et al., 2013; Parkinson, 2013; Domínguez-Rodrigo et al., 2014). Small and large bovids in both assemblages have high Shannon's evenness indices for skeletal parts likely to survive density-mediated destruction, suggesting that nearly complete carcasses were transported on-site (Faith et al., 2009; Ferraro et al., 2013). This is not only consistent with early carcass access, but also suggestive of hunting because small bovid remains are rapidly destroyed by carnivores (Schaller, 1968; Blumenschine, 1986; Ferraro et al., 2013). Most studies of both Kanjera and FLK-Zinj report cut and tooth mark frequencies similar to those produced in hominin-to-carnivore access experiments (Domínguez-Rodrigo and Barba, 2006, 2007; Ferraro et al., 2013; Parkinson, 2013; Domínguez-Rodrigo 2014; but see Blumenschine, 1995; Blumenschine et al., 2007; Pante et al., 2012, 2015). Cut mark locations and frequencies from both sites are consistent with processing of fleshy carcasses, indicating early access (Bunn and Kroll, 1986; Oliver 1994, 2015; Domínguez-Rodrigo et al., 2007; Ferraro et al., 2013; Parkinson, 2013).

A recent analysis of FLK-Zinj bovid age frequencies indicates hominins practiced hunting (Bunn and Pickering 2010a; Bunn and Gurtov, 2014). This analysis builds on previous approaches comparing faunal age frequencies from zooarchaeological assemblages with those created by carnivores to understand hominin carcass acquisition strategies (Klein, 1978, 1982). Stiner (1990) noted that, because prey age is related to predator search and acquisition strategies, comparative analysis of mortality patterns created by carnivore predation and well-understood human formed assemblages should help in interpreting the carcass acquisition behavior of extinct hominins. She condensed prey ages to three meaningful categories (juvenile, prime adult, and old adult) and used ternary diagrams to compare mortality profiles created by natural attrition, carnivores, and human hunting. She showed that ambush and cursorial carnivores create distinctive prey age frequencies that plot in different regions of the ternary diagram (Fig. 1). Stiner's (1990) comparison of Native American and Middle and Upper Paleolithic zooarchaeological samples with carnivore-created mortality samples revealed that the hominin-created samples are similar to those of ambush predators, indicating that many prehistoric hunters also practiced ambush hunting.

Bunn and Pickering (2010b) defined a new method to categorize juvenile, prime adult, and old bovids using African bovid tooth wear and eruption data, relating bovid age classes to changes in vulnerability to predation. They used Steele and Weaver's (2002) modified triangular plot software to graph bovid mortality profiles created by carnivores, the FLK-Zinj hominins, and a pooled sample of three fossil accumulations from Bed I Olduvai Gorge (FLK-N 1-2, FLK-N 6, and FLK-NN 2), a 'background' assemblage argued to result from felid predation (Bunn and Pickering, 2010b). They tested several hypotheses about how FLK-Zinj hominins acquired bovid carcasses using carnivore-created mortality samples (Schaller, 1972; Kruuk, 1972; Spinage, 1982) as a baseline and eliminated young juveniles from analyses due to presumed fossil preservation biases (Bunn and Pickering 2010b). Their analyses revealed that Oldowan hominins were not scavenging large felid kills because the FLK-Zinj large bovid mortality sample contains a high frequency of prime adults, unlike their lion-created mortality profile that closely resembles a population living structure. They argued that FLK-Zinj hominins were ambush hunters using woodland concealment opportunities to acquire prime adults. They further argued that the lack of similarity with juvenile dominated profiles created by cursorial carnivores disproved the Bramble and Lieberman (2004; see also Lieberman et al., 2007) hypothesis that early hominins engaged in endurance running during persistence hunting (ER-PH) to acquire prey.

We can reasonably predict that habitat differences impacted Oldowan hominin diets (Plummer, 2004) because diets of animals such as extant *Papio* spp., *Pan* spp., and other primates vary by habitat (Brown and Zunino, 1990; Hill and Dunbar, 2003; Ganas et al., 2004; Moore et al., 2017). Differences in seasonality, habitat structure, and characteristics of plant and animal communities would offer different food choices and present different hunting and scavenging opportunities to hominins active in different ecosystems (e.g., Blumenschine, 1986; Peters and Blumenschine, 1995; Plummer, 2004). While a consensus that Oldowan hominins at FLK-Zinj and Kanjera had early access to meat-rich carcasses continues to develop, we have little insight into how varied habitats might have affected carcass acquisition strategies.

Here we provide the bovid mortality data from Kanjera South, Kenya. We compare it to the FLK-Zinj and Olduvai 'background' bovid mortality patterns, and compare each fossil assemblage to those created by modern African carnivores that occupy different habitats and use different hunting strategies. We use analyses of these data to evaluate proposed modes of hominin carcass acquisition, including scavenging, hunting, and Bramble and Lieberman's (2004) ER-PH model to test the hypothesis that variation in habitat structure played a major role in Oldowan hominin prey acquisition.

1.1 Kanjera South and FLK-Zinj paleoenvironments

Kanjera South and FLK-Zinj preserve different habitats. Hominin activities at Kanjera South occurred in an open, grassy setting on the margins of a lake basin and are preserved in primary depositional context (Behrensmeyer et al., 1995; Ditchfield et al., 1999, 2018; Plummer et al., 1999, 2009a, b). Hominins were attracted repeatedly to the site, where alluvial deposition, contemporary with and/or following hominin activities, created a 3 m-thick sequence of alluvial sands and silts in Beds KS-1 to KS-3. Minimal bone weathering indicates that fossils and artifacts were buried rapidly after they were discarded by hominins (Ferraro, 2007; Ferraro et al., 2013). Field observations and granulometric analysis of the fine sediment fraction, a lack of rounding of bones and artifacts in conjunction with taphonomic analysis indicate that archaeological material in Beds KS-1 to KS-3 were largely undisturbed by water flow (Ditchfield et al., 2018).

Grassy habitats were well represented in local and regional Kanjera plant palaeocommunities. Soil carbonates have $\delta^{13}C$ values indicative of >75% grass, within the range of open to wooded grasslands today (Plummer et al., 2009b). Equids and antelopes whose living relatives prefer open settings dominate the faunal sample (Plummer et al., 1999). Stable carbon isotopic analysis of enamel indicates that these taxa had diets composed predominantly of C_4 plants, again reflecting the dominance of grass in the plant community (Plummer et al., 2009b). Water-dependent taxa *Hippopotamus*, *Crocodylus*, and reduncine bovids are rare but reflect the nearby presence of water.

Geological, phytolith, biomarker, and faunal analyses, as well as stable isotopic analyses of pedogenic carbonates and of antelope tooth enamel collectively indicate that FLK-Zinj formed in a wooded setting (Plummer and Bishop, 1994; Sikes, 1994; Ashley et al., 2010a, b; Blumenschine et al., 2012; Magill et al., 2016), most likely in a broad area of groundwater woodlands mixed with wooded grasslands near a pond (Arráiz et al., 2017; Domínguez-Rodrigo et al., 2017). Woody dicot and other forest/woodland indicators dominate the FLK-Zinj phytolith samples (Ashley et al., 2010a; Arráiz et al., 2017) testifying to the presence of dense, well-watered woodlands, concordant with bovid tribal frequencies similar to those found in modern wet woodlands like Fina, Mali, and Kainji, Nigeria (Plummer et al., 2009b). Unlike the grassland diet indicated by enamel isotopes of Kanjera *Antidorcas recki*, *A. recki* from FLK-Zinj have an isotopic signal indicative of a mixed diet of browse and grass (Plummer et al. 2009a). Freshwater snails, urocyclid slugs (Hay, 1973), *Galago*, and the acacia rat *Thallomys* (Jaeger, 1976; Gentry and Gentry, 1978) provide additional indication of woodland habitats at FLK-Zinj. Bovids that prefer dry (*Parmularius altidens, Connochaetes* sp., *Oryx* sp.) or fresh (*Kobus sigmoidalis*) grass represent 73% of the aged bovid assemblage reported by Bunn and Pickering (2010a). Thus, grassy woodland habitats were likely another component of the broader Bed I floral paleocommunity.

Archaeological finds from FLK-Zinj derive from a 10 cm-thick waxy clay unit (Leakey, 1971), though some material comes from below this main level (Domínguez-Rodrigo et al., 2010). Fossils are generally fresh with minimal weathering, suggesting that the assemblage accumulated and was buried on the order of 5–10 years (Potts, 1986, 1987, 1988), or perhaps much less (Bunn and Kroll, 1986, 1987). Hominin activities at the Kanjera South locale occurred for decades to centuries in a rapid sedimentary regime with episodic traces of hominin activity buried by seasonal alluviation. The sites' depositional contexts are complimentary, with FLK Zinj representing a narrow temporal window and Kanjera documenting persistent hominin activities over a longer period.

1.2 Habitat structure and carnivore-created bovid mortality patterns

Habitat structure is the physical architecture of an ecosystem that animals interact with, including topographic and geological features as well as the types and distributions of plants (McCoy and Bell 1991). It is a defining factor in an animal's niche space and behavioral ecology (Whittaker, 1975). For carnivores it plays a critical role in predator-prey dynamics, mode of predation, likelihood of hunting success, where young are raised, and degree of interspecific competition (Stephens and Peterson, 1984;

Fitzgibbon, 1990; Gros and Rejmánek, 1999; Theuerkauf et al., 2003; Hopcraft et al., 2005; Trap et al., 2008; Jackson et al., 2014).

Opportunities and constraints in each stage of predation—search, encounter, kill, and consumption—are all a function of habitat structure (Endler, 1986). Wildlife studies demonstrate ambush predators rely on a variety of structural features such as trees and bushes, tall grass, deep snow, and erosional gullies to facilitate prey acquisition. Serengeti lions, for example, not only favor ambush locations (e.g., near water, in woodlands) where prey is easy to catch over locations with high prey density, their hunting success rates are significantly greater in locations with concealment opportunities (Hopcraft et al., 2005). Alteration of the landscape following fire in Kafue National Park underscores the importance of concealment opportunities for lions. Fire forced most bovids to move into the grasslands, but Kafue lions remained in woodlands and began hunting buffalo rather than following their favored prey onto grasslands (Mitchell et al., 1965). Leopards strongly prefer wooded habitats to ambush and store prey (Bertram, 1999; Hayward et al., 2006). Ambush predators that lie in wait for prey to pass nearby sample age groups in proportions equivalent to standing populations, creating mortality patterns that contain many prime adults and approximate the age structure of living populations (Stiner 1990; Fig. 1).

Open habitats do not provide opportunities for ambush as do structurally complex habitats, so cursorial predators living in open habitats target prey disadvantaged in speed and/or stamina (Wilson and Mittermeier, 2009). Predation in open habitats frequently requires bouts of running, either at high speeds over short distances (e.g., cheetahs) or endurance running over longer distances often by multiple group members (e.g., spotted hyenas and wild dogs). Patches of cover can aid hunting in open habitats by allowing predators to get closer to their prey in the search/encounter stage. For example, cheetahs in the Karamoja Region, Uganda prefer grasslands with 51–100 cm high grass when stalking prey (Gros and Rejmánek, 1999). In areas with grass height less than 30 cm, cheetah hunting success was reduced threefold, likely due to the lack of cover (Fitzgibbon, 1990). Open habitats also give carnivores an expansive field of view offering opportunities to observe behavioral cues to prey vulnerabilities and reduce chances of unsuccessful hunts. Juvenile prey are particularly vulnerable as they are naïve and have less endurance making them relatively easy to run down. Juveniles of some species can be captured where their mothers have cached them. Consequently, carnivores occupying open habitats create juvenile-dominated mortality profiles that fall in the attritional zone of ternary diagrams (Fig. 1).

1.3 Research questions

We expect that habitat structure influenced Oldowan hominin predatory strategy in ways similar to how it influences the predation behaviors of modern carnivores. If this were the case, the Kanjera bovid mortality profiles would differ from those documented by Bunn and colleagues for FLK-Zinj in ways similar to the differences between modern cursorial and ambush predator profiles. Our specific expectations are:

1) If the open grasslands at Kanjera influenced hominin carcass acquisition behaviors, then bovid mortality should be similar to that created by modern cursorial predators that create juvenile-dominated assemblages.
2) If Kanjera hominins engaged in ambush hunting then the small bovid mortality samples should include higher frequencies of adults like mortality samples created by carnivores occupying structurally complex habitats.

Expectations for the Kanjera large bovid mortality pattern are more complicated, as taphonomic analysis suggests they were acquired through passive scavenging as well as early access to some carcasses through hunting or confrontational scavenging. We have two possible expectations concerning whether or not large bovids were acquired mainly through scavenging carnivore kills or through a mix of scavenging and hunting:

3) If Kanjera hominins primarily scavenged large bovids, then the mortality profile should be similar to those created by one or more modern carnivores active in open habitats.
4) If Kanjera hominins employed a mixed strategy hunting and scavenging large bovids, the mortality pattern should be dissimilar to modern carnivore-kill samples as it could include scavenging from both ambush and cursorial carnivores.

Much of the debate on Oldowan carcass acquisition behavior has been based on analysis of just one site, FLK-Zinj. The Kanjera data are significant for providing another sample for investigating Oldowan hominin foraging ecology in a novel open habitat setting (Plummer et al., 2009a). Irrespective of the hominin species forming the two assemblages, comparison of Kanjera and FLK-Zinj Oldowan zooarchaeological mortality profiles with those created by extant ambush and cursorial carnivores offers a way to examine variability in hominin prey acquisition strategies when assessed with reference to constraints and opportunities provided by habitat structure.

2. Methods

We used previously published methods to ensure comparability between data from FLK-Zinj and Kanjera South. Bovid size class definitions follow live weights given by Bunn (1986) and Bunn and Kroll (1986). Bunn and Pickering (2010a, b) defined five age categories (young juvenile, subadult, early prime adult, late prime adult, and old adult) based on bovid tooth eruption and wear and their definition of the prime adult-old threshold based on their assessment of old individual vulnerabilities (Table 1).

All bovid premolars and molars in maxillary and mandibular specimens, as well as isolated teeth recovered from Kanjera South Beds 1-3 in 1995 to 2015 were examined (*n* = 125). Our taxonomic identifications of the Kanjera fauna were based on comparisons with modern and fossil bovids housed at the National Museum of Kenya in Nairobi. Each tooth was scored for eruption stage (not erupted, erupting, fully erupted, in wear) and degree of infundibulum wear (none, minimal, heavy, worn away), and assigned to an age class using the Bunn and Pickering (2010b) scheme (Table 1). The minimum number of individuals (MNI) in each size class was calculated for each bed using tooth wear, eruption, and size within a taxonomic category. We combined specimens from KS Beds 1–3 to increase sample size for this analysis because taphonomic analyses showed no differences in accumulation processes (Ferraro, 2007; Ferraro et al., 2013), and mortality sample confidence intervals (CI) overlap substantially. Teeth in the thin conglomerate facies KS-2CP were not included, as their accumulation may have been influenced by water flow (Plummer et al., 1999; Ditchfield et al., 2018).

We compared the Kanjera mortality frequencies to 1) the FLK-Zinj mortality sample, 2) a pooled set of three Olduvai assemblages (FLK-N 1-2, FLK-N 6, and FLK-NN 2) thought to have formed without hominin involvement (Table 2), and 3) to modern bovid mortality samples created by lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*), cheetahs (*Acinonyx jubatus*), and wild dogs (*Lycaon pictus*) (Table 3). The modern carnivore data were also used to assess variation in mortality profiles created by the same carnivore species at different locations and to evaluate whether mortality patterns distinguish between ambush and cursorial predators.

To assess possible age preferences of animals taken by carnivores and Oldowan hominins, we use standing age structures of 11 African bovid populations (2 impala, 2 kudu, 4 wildebeest, 1 buffalo, 1 waterbuck and 1 eland; Table 4). Age classes provided in these studies are not exactly equivalent to the tooth wear and eruption scheme (Table 1), but do provide an indication of overall age structure.

As originally devised (Stiner 1990), ternary plot mortality profile analysis did not account for sample size, and individual samples could not be compared statistically. We use Weaver et al.'s (2011) updated ternary plot software for comparative analyses of mortality frequencies. This software uses likelihood statistics to plot 95% CIs around the sample mean and works with samples in which one age class is empty. Bunn and Pickering (2010a, 2010b) and Bunn and Gurtov, (2014) used Steele and Weaver's (2002) modified triangular plot program for their analyses. Both methods give comparable results. χ^2 and Fisher's exact tests performed with SYSTAT v. 13 (Systat Software, San Jose) were used for some comparisons to highlight central trends.

3. Results

The Kanjera dentognathic minimum number of individuals (MNI) is 62, comprised of 22 small bovids (35.5%) and 40 large bovids (64.5%) (Table 2). The FLK-Zinj dentognathic MNI is 26, composed of 7 small (26.9%) and 19 large (73.1%) bovids. The Kanjera small bovid assemblage is dominated by juveniles (50%, *n* = 11), of which 63.6% (*n* = 7) are young juveniles. Juveniles make up only 14.3% (*n* = 1, a subadult) of the FLK-Zinj small bovid sample. Old individuals are uncommon in the Kanjera small bovid sample (13.6%, *n* = 3), but are the most common FLK-Zinj small bovid (71.3%, *n* = 5). As with small bovids, 50% (*n* = 20) of the Kanjera large bovids are juveniles. Not only is this almost twice the frequency of juveniles seen in the FLK-Zinj large bovid assemblage (26.3%, *n* = 5), young juveniles are twice as common in the Kanjera assemblage (20%, *n* = 8 vs. 10.5%, *n* = 2). In the FLK-Zinj large bovid sample, prime adults predominate (63.2%, *n* = 12). At Kanjera, prime adults comprise 45% (*n* = 18) of the large bovid sample and so rank behind juveniles. Old individuals are the least common age group in both assemblages, but are over twice as common in the FLK-Zinj sample (10.5%, *n* = 2) as they are at Kanjera (5%, *n* = 2).

Bunn and Pickering (2010b) recommend excluding young juveniles from the analysis of fossil assemblages because of potential density-mediated destruction of their relatively fragile bones. This exacerbates a drawback of the ternary plot method that causes results to be highly sensitive to age class definitions in small samples. Moreover, excluding juveniles is not warranted in our case because of the high frequencies of young juveniles in Kanjera small and large bovid samples (Table 1; Figs. 1c and 2a) and taphonomic analyses (Ferraro, 2007) suggest that there is not a strong preservation bias against young juveniles. Bunn and Pickering (2010a) noted the presence of two very young juvenile (perhaps fetal) large bovids in the FLK-Zinj assemblage and five young juveniles in the Olduvai background assemblage, suggesting that density-mediated attrition was not significant in these fossil assemblages either. Young juveniles make up a large proportion of small and large bovid kills made by modern carnivores (Table 3). Excluding young juveniles leads to a substantial shift of the carnivore samples towards the prime corner of the ternary plot, biasing the analysis towards this age category (Fig. 2b, d). For these reasons we included young juveniles in our analysis.

3.1 Variability in carnivore-created mortality patterns

Habitat-related variation in ecological factors such as prey diversity, predator and prey populations, and carnivore guild structure could result in differences in the age structure of the bovid prey killed by one carnivore species in different locations. Although the number of wildlife studies using comparable aging methods to report bovid mortalities created by carnivores is small (*n* = 18; Table 3; Supplementary Online Material [SOM] Fig. S1), evaluation of this variability is a prerequisite for their use in interpreting zooarchaeological mortality patterns. They also allow us to compare the mortality profiles made by ambush predators with those made by cursorial predators.

There is no significant difference in the small bovid mortality profiles of prey killed by different populations of one carnivore species (Tables 3 and 5; SOM Fig. S1a–e). This justifies pooling the small bovid prey data by carnivore species to evaluate species-specific bovid mortality frequencies (Fig. 2). There is some variation in large bovid mortality profiles created by different lion, wild dog, and spotted hyena populations (Tables 3 and 5; SOM Fig. S1f, h, j). A χ^2 test shows that Kafue lions take significantly more prime adult large bovids than do Serengeti lions, which exhibit a preference for juveniles (Tables 3 and 5). This might reflect the Serengeti's more open habitat compared to Kafue. Both wild dog populations prefer juveniles (Serengeti, 100.0%, Kafue, 57.7%) and the significant difference between the samples by χ^2 test is due to the absence of adults in the Serengeti sample (Tables 3 and 5). The Serengeti and Ngorongoro Crater hyena-kill samples are significantly different (Table 5) due to a greater proportion of juveniles in the Ngorongoro sample and higher frequencies of prime and old adults in the Serengeti (Table 3). Nevertheless, even with these few differences in age class values, when samples from the same species are plotted in ternary diagrams they fall in the same region and the CI margins are overlapping or in contact (lion-kill samples) or the samples are dominated by the same age category (young juveniles in wild dog-kill samples; SOM Fig. S1). It is therefore reasonable to pool the large bovid mortality samples by carnivore species (Fig. 2).

Pooling the carnivore-kill samples by species confirms expectations for how carnivores living in different habitats sample prey populations. Cursorial predators all show a preference for young juvenile small bovid prey compared to prime adults (hyenas, 42.9% vs. 35.7%; cheetah, 63.2% vs. 24.4%; wild dog, 51.4% vs. 39.8%; Fig. 2a; Table 3). The results are somewhat different for small prey mortality samples created by ambush predators. Prime adults are most common in the combined Serengeti, Kafue, and Rwenzori small bovid sample taken by lions (45.5%). Likewise, prime adults dominate the summed Serengeti and Kafue leopard-kill small bovid sample (49.4%). Consequently, small bovid mortality values for both ambush predators plot in the ‘living structure zone’ of the triangular plot, whereas those of cursorial predators plot in the ‘attritional zone’ because of their higher juvenile frequencies.

The general pattern of cursorial predators killing small bovid juveniles most frequently and ambush predators taking more prime adults holds true for large bovids as well. The combined Serengeti and Kafue wild dog-kill sample is comprised of significantly more young juveniles (87%) than subadult juveniles (3%), prime adults (5%) or old individuals (5%). Spotted hyenas also kill more young juveniles (52.7%) than prime adults or old individuals. In contrast, prime adults are most common in the combined Serengeti, Rwenzori, and Kafue lion-kill sample (35.4%). The lion, hyena, and wild dog prey samples are all significantly different from each other, as demonstrated by their non-overlapping CIs in the ternary diagram (Fig. 2c).

3.2 Ambush vs. cursorial carnivore mortality profiles

A closer look at the mortality profiles of ambush and cursorial predators may provide insight into hominin predatory behavior (e.g., Stiner, 1990; Bunn and Pickering, 2010a; Bunn and Gurtov, 2014). For small bovids, with the exception of the cheetah-kill CI contour, which is separate from both lion and leopard CIs, all of the CIs of bovids killed by ambush (lions and leopards) and cursorial (hyenas and wild dogs) predators overlap (Table 3, Fig. 2a). However, the observed prey mortality values are separated in the plot, with cursorial taxa plotting in the attritional zone of the diagram and ambush taxa plotting in the living structure zone. Additionally, χ^2 tests indicate significant differences in the proportions of small bovid juveniles, prime adults, and old individuals in most pairwise comparisons of ambush and cursorial predators (leopard-kills vs. hyena-kills, $n = 177$, $\chi^2 = 6.33$, $p = 0.0422$; leopard-kills vs. cheetah-kills, $n = 288$, $\chi^2 = 16.74$, $p = 0.0002$; lion-kills vs. cheetah-kills, $n = 422$, $\chi^2 = 28.5$, $p = 0.0001$; lion-kills vs. wild dog-kills, $n = 320$, $\chi^2 = 7.46$, $p = 0.0240$). χ^2 and Fisher's exact tests also demonstrate significant differences in the proportions of large bovid prey killed by ambush and cursorial predators (lions vs. hyenas, $n = 664$, $\chi^2 = 49.47$, $p = <0.0001$; lions vs. wild dogs, $n = 487$, $\chi^2 = 74.64$, $p = <0.0001$; leopards vs. wild dogs, $n = 113$, $p = 0.0026$, Fisher's exact test). Because this mortality profile patterning reflects hunting mode, we combined bovid age frequencies for lions and leopards and those for hyenas, cheetahs, and wild dogs to create large ambush and cursorial predator samples (Fig. 3). This is justified because there are few differences between the ambush predators (Table 5) and although some pairwise comparisons among cursorial predators showed significant differences, their values all plot in the attritional zone of the ternary plot (SOM Fig. S1). The resultant ambush and cursorial carnivore sample CIs do not overlap and are therefore significantly different (Fig. 3a; Table 5). As expected, the cursorial predator CI for small bovids falls into the attritional region of the plot, whereas that of small prey taken by ambush predators plots largely within the living structure region (Fig. 3a). For large bovid prey, the cursorial and ambush predator CIs are again well-separated, but the ambush predator age proportions value and much of its CI lie on the edge of the attritional zone, rather than in the living structure zone of the ternary diagram (Fig. 3b). In part, this reflects the high frequency of juveniles in the Serengeti lion-kill sample.

3.3 Kanjera South vs. Olduvai vs. carnivore-created mortality patterns

Several patterns characterize differences between the fossil assemblages and the carnivore-kill samples. Considering small bovids first, juveniles are much more common at Kanjera (50.0%) causing its CI to fall mainly within the attritional region of the ternary plot, whereas old individuals dominate the FLK-Zinj small bovid sample (71.4%; Table 2, Fig. 2a). Although the Kanjera and FLK-Zinj CIs overlap slightly, they are situated in different regions of the ternary plot and their proportions of juveniles, prime-adults, and old individuals are significantly different ($n = 29$, $p = 0.0156$, Fisher's exact test; Table 5). The Kanjera small bovid CI circumscribes those for all modern carnivores (Figs. 2a and 3a). However, the Kanjera age category proportion value falls in the attritional area and is more similar to the cursorial values due to their shared high frequencies of young juveniles (Table 5; Fig. 2a). In contrast, the FLK Zinj small bovid sample CI, due to its unusually high proportion of old individuals, is significantly different from both the pooled ambush and cursorial samples. Although all small bovid carnivore-kill CIs, save that for cheetahs, intersect the Olduvai background CI, Fisher's exact test shows that the age class frequencies for the Olduvai background differ significantly from cursorial hyenas ($n = 118$, $p = 0.0246$) and wild dogs ($n = 127$, $p = 0.0131$). The pooled cursorial-kill and

Olduvai background CIs are significantly different (Fig. 3a; Table 5). CI ellipses for the ambush predators (lions and leopards) are not significantly different from each other or the Olduvai background as prime adults dominate all three samples (Figs. 2a and 3a).

For large bovids, the Kanjera, FLK-Zinj, and Olduvai background CIs all overlap (Fig. 2c). Fisher's exact tests of these assemblages show that their age class proportions are not significantly different (Kanjera vs. FLK-Zinj, $n = 59$, $p = 0.2242$; Kanjera vs. Olduvai background, $n = 74$, p = 0.3172; FLK-Zinj vs. Olduvai background, $n = 53$, $p = 0.6123$). The Kanjera mortality sample, however, appears more similar to the cursorial carnivore samples, whereas the FLK-Zinj sample is more similar to those created by ambush carnivores. For example, the hyena-kill CI overlaps the Kanjera CI, but the FLK-Zinj sample does not (Fig. 2c). The opposite is true for the lion-kill sample, which overlaps FLK-Zinj but not Kanjera. The age class proportion values of the lion and FLK-Zinj samples are significantly different ($n = 406$, $\chi^2 = 6.09$, $p = 0.0476$), largely because of the greater frequency of prime adults in FLK-Zinj (63.2% vs. 35.4%). Cheetah and leopard samples are too small to interpret, but the large wild dog sample falls in the attritional zone with the Kanjera mortality sample. Comparison with the pooled ambush and pooled cursorial carnivore samples also indicates that the FLK-Zinj mortality pattern is more similar to ambush carnivores as their CI ellipses overlap (Fig. 3b). The Kanjera mortality sample, however, is significantly different from both pooled carnivore samples.

The Kanjera, FLK-Zinj, and Olduvai background CIs all overlap (Figs. 2c and 3b). Except for the wild dog-kills, all carnivore large bovid CIs overlap the Olduvai background assemblage CI (Fig. 2c). The Olduvai background and the pooled ambush carnivore sample CIs intersect and are not significantly different, but the Olduvai background differs significantly from the pooled cursorial sample (Fig. 3c; Table 5).

Because of differences in aging techniques and uncertainty over how various researchers have classified subadults and old individuals, known age class frequencies of most modern bovid populations (Table 4) cannot be equated directly to the fossil or carnivore-kill assemblages. That being said, some comparisons are useful to identify broad similarities and differences between fossil assemblages and standing bovid populations. Impala (*Aepyceros melampus*) standing populations from Akagera National Park, Rwanda (Spinage, 1972) and from southern Zimbabwe (Dasmann and Mossman, 1962) contain between 31.7% and 44.4% juveniles, respectively (Table 4). If representative of the range of juvenile frequencies in small bovid populations, the Kanjera small bovid sample contains as much as 18.3% more juveniles than might be expected. In contrast, FLK-Zinj contains 17.4–30.1% more adults than the standing small bovid populations. Juveniles are 11.7–24.4% less frequent in the Olduvai background than these two modern impala populations. On average, the 16 standing large bovid population samples are comprised of 34.4% juveniles (range = 19.7–63.2%) and 65.6% adults (range = 36.8–76.1%; Table 4). Kanjera contains 16.6% more juveniles than the average standing large bovid population, whereas FLK-Zinj has 8.1% less than might be expected. The proportion of juveniles in the Olduvai background and the average of standing large bovid populations are similar.

4. Discussion

Our overall expectation that habitat structure influenced Oldowan hominin predation practices in ways similar to carnivores was met. Hominins occupying grasslands at Kanjera South took high frequencies of young juvenile small bovids as is common with modern carnivores hunting in open habitats (Tables 2 and 3; Figs. 2a and 3a). The Kanjera small bovid CI circumscribes all those of cursorial carnivores and is most similar to the pooled cursorial sample. Like the cursorial carnivore-kills, Kanjera contains considerably more juveniles than found in standing small bovid populations. In contrast, hominins forming the FLK-Zinj assemblage took high frequencies of adult small bovids, in this case a uniquely high frequency of old individuals (Bunn and Pickering, 2010a; Bunn and Gurtov, 2014; Table 3; Figs. 2a and 3a).

Large bovid mortality samples from both Oldowan sites also vary in ways consistent with habitat specific differences in prey acquisition (hunting in the open versus ambush hunting in woodlands; Tables 2 and 3; Figs. 2a and 3a). The Kanjera mortality frequencies clearly trend towards the juvenile end of the ternary plot and the Kanjera bovid age class proportion value and most of its CI falls in the attritional zone that characterizes mortality samples created by cursorial carnivores. However, the Kanjera large bovid CI is significantly different from both the pooled cursorial and pooled ambush carnivore samples. The Kanjera mortality sample is dissimilar to those from Middle Paleolithic and North American zooarchaeological faunas believed to have accumulated through ambush hunting, or ethnoarchaeological faunas created by ambush hunters (Stiner 1990; Bunn and Gurtov 2014). The FLK-Zinj large bovid sample displays nearly the opposite pattern. Its age class proportion value and most of its CI falls in the living structure zone of the ternary diagram, and its CI overlaps that of lions and the pooled sample of ambush carnivore-kills. It includes considerably more prime adults than the Kanjera sample, and because of its high prime frequency its age class proportions are significantly different from the pooled ambush carnivores (Tables 2 and 5; Figs. 2c and 3b). In fact, the prime dominated FLK-Zinj large bovid assemblage is similar to those created by Middle Paleolithic, North American, and modern Hadza ambush hunters (Bunn and Pickering, 2010b; Bunn and Gurtov, 2014).

Carcass acquisition at Kanjera South The taphonomic and mortality data for the Kanjera small bovid assemblage support an interpretation of hunting. The small bovid mortality sample is more variable than that created by any single carnivore. This might suggest hominins were scavenging carnivore kills, but several facts make this unlikely. Fresh, carnivore-killed carcasses would be rarer than potentially vulnerable juvenile bovids (Tooby, 1987). Observations of carnivore-kills demonstrate that carnivores in grassland settings quickly consume small bovid carcasses (e.g., Schaller, 1968; Blumenschine, 1986, 1987). The Kanjera fossil assemblage includes carnivores capable of destroying juvenile bovid carcasses (the hyenid *Crocuta ultra*, a large felid, and a size 2 carnivore; Bishop et al., 2006). These data suggest that scavenging opportunities were limited at Kanjera. Moreover, taphonomic and zooarchaeological analysis (Ferraro et al., 2013; Parkinson, 2013) do not support an interpretation that small bovids were scavenged. Cut marks distributed across meaty portions of small bovid limbs, evidence for marrow processing, low tooth mark frequencies consistent with early access models, and the relatively even representation of high survivorship parts across the skeleton are consistent with hominins hunting, transporting, and butchering complete or nearly complete small bovid carcasses at Kanjera South.

The Kanjera large bovid mortality and taphonomic data present a more complex pattern. Kanjera large bovid skeletal part representation is biased in ways suggestive of selective hominin transport, rather than the transport of complete carcasses as seen in adult and juvenile small bovids (Ferraro et al., 2013). Limb bones of large bovids are relatively common compared to axial elements, and proximal and intermediate long bones are more abundant than metapodials. These proportions are not driven by the differential destruction of large mammal axial elements, as the bones of smaller, more fragile size 1 and 2 bovids are well preserved on site. Moreover, large bovid crania and mandibles are the most common elements and some show percussion damage related to brain and mandibular pulp extraction. This overrepresentation of large bovid limbs and particularly heads suggests that Kanjera hominins acquired at least some of the large bovid assemblage through scavenging (Ferraro, 2007; Ferraro et al., 2013).

The Kanjera large bovid sample contains nearly equal frequencies of juveniles and prime adults; although its age proportions value plots in the attritional zone of the ternary diagram, its CI straddles the attritional and living structure zones. The Kanjera CI overlaps with those from the spotted hyena, cheetah, and leopard, though the CIs of the latter two are large due to small sample sizes and so should not be given undue weight. The overlapping CI with the spotted hyena sample is consistent with Expectation 3 suggesting the possibility that large bovids were being scavenged in various states of completeness. The low frequency of toothmarks (Ferraro et al., 2013:Table S2, average of all analysts' observations = 9.8%; Parkinson, 2013:Table 3.4, 13.8%) and bone breakage attributable to carnivores in the large bovid assemblage argues against Kanjera hominin reliance on scavenging. The Kanjera large bovid sample is distinct from the pooled mortality samples created by both cursorial and ambush predators (Fig. 3b). This is consistent with a variable hominin strategy for acquiring large bovids, perhaps combining hunting of juveniles and the scavenging of adult carcasses (Expectation 4).

Carcass acquisition at FLK Zinj The high frequency of old bovids in the size 1–2 bovid sample at FLK-Zinj is a unique finding (Bunn and Pickering 2010a). No modern carnivore exhibits this strong preference for old individuals, which are relatively uncommon in living antelope populations. Overall, the FLK-Zinj small bovid sample contains a higher proportion of adults than do live impala populations. Scavenging of carnivore kills is thus unlikely to have yielded such a skewed age distribution. Bunn and

Pickering (2010a) argued that ambush hunting in woodlands is the most likely explanation because old gazelles prefer woodlands. Solitary mature males are a common occurrence in many social bovid taxa, and because they forage at the edge of groups or alone, they are more vulnerable to predation (Bigalke, 1970; Estes, 1967, 1991). The evidence suggests that Oldowan hominins at both Kanjera and FLK-Zinj exploited vulnerable small bovids—juveniles that were less likely to evade hunters in the open at Kanjera, and peripheral old males at FLK-Zinj.

Bunn and Pickering (2010a) and Bunn and Gurtov (2014) argued that FLK-Zinj hominins acquired large bovids through ambush hunting. The FLK-Zinj large bovid sample contains more prime adults than even the pooled sample of ambush predator-kills and differs significantly from the pooled cursorial predator-kills. We agree with Bunn and Pickering (2010a) and Bunn and Gurtov (2014) that the similarity with bovid mortalities produced by the Hadza, and also in evidence in later zooarchaeological assemblages, indicates ambush hunting of prime-adults by FLK-Zinj hominins.

That said, reconsidering hominin early access to carcasses by power scavenging at FLK-Zinj seems prudent. Power or confrontational scavenging, where carnivores were driven from carcasses that retained most or all of their flesh, was considered plausible by Bunn and Pickering (2010a), but later discarded for a hunting-focused model by Bunn and Gurtov (2014). Our analysis shows the FLK-Zinj large bovid CI overlaps with a) the CIs from the pooled ambush predator sample, b) the Olduvai background sample probably formed by felids (Domínguez-Rodrigo et al., 2007), c) the Kafue lion-kill sample, and d) the Kanjera large bovid sample that we argue includes scavenged remains (Figs. 2b and 3b; SOM Fig. S1f). Examples of damage on deer bones consumed by captive lions and tigers similar to damage on fossils found at FLK-Zinj also supports carcass acquisition by power scavenging (Parkinson et al., 2015). Some sabertooth species were likely solitary ambush hunters in woodlands (Lewis and Werdelin, 2007; Werdelin and Lewis, 2013) and may have been vulnerable to having their kills stolen by a hominin foraging group. It seems that some of the fleshy carcasses butchered at FLK-Zinj were stolen from carnivores.

4.1 Environmental constraints and opportunities for Oldowan hominin foraging

Our analyses show that Kanjera South and FLK-Zinj assemblages differ in the sizes and mortality profiles of the bovids that were hunted and scavenged. A major distinction between the two localities is habitat structure, with little evidence of tree cover on the Kanjera South grassland, and greater habitat complexity and greater possibilities of tree cover in the FLK-Zinj woodlands. This suggests the possibility that Oldowan hominins varied their hunting strategies to suit their environmental setting.

It is therefore useful to examine some aspects of extant carnivore predation behavior and prey vulnerabilities to reconstruct possible Oldowan hominin foraging strategies in different habitats. A factor in determining hunting success for modern carnivores is the predetection predator-to-prey distance: the closer a predator can get to its prey before detection, the greater the likelihood of hunting success (Elliot et al., 1977; Orsdol 1984; Caro, 1986; FitzGibbon and Fanshawe, 1988). Predetection predator-to-prey distance is influenced by factors such as the presence of effective vegetation cover and the habits of prey species. In structurally heterogeneous habitats, ambush predators use cover to reduce predetection distance. Bunn and Pickering (2010a) and Bunn and Gurtov (2014) argue that proximity to prey before detection would have been necessary for successful hunting by hominins, and that FLK-Zinj woodlands would have afforded hominins concealment to ambush large bovids.

Conversely in open habitats with increased visibility, prey will detect predators at a greater distance. Open habitat predators maximize their chances for a successful pursuit by a) observing prey to assess which individuals are most vulnerable, and b) stalking to minimize distance to prey. Even for cursorial predators like cheetahs, close proximity prior to pursuit results in greater success (Caro, 1986,1995). The overlap of the Kanjera small bovid CI with that of the pooled ambush carnivore sample in the living structure zone of the ternary diagram is consistent with hominins also having an effective strategy for capturing prime adult small bovids in the open. Tall grass provides ambush opportunities for lions across Africa (Schaller, 1972; Elliot et al., 1977; Orsdol, 1984; Stander, 1992; Tappen, 1995) and grassland microhabitats at Kanjera may have provided concealment to acquire less vulnerable bovid adults.

Overall, the Kanjera South grasslands would have offered minimal cover and, like cursorial carnivores, Kanjera hominins may have exploited aspects of small, particularly juvenile, bovid behavior when hunting. Young gazelles will flee for a short distance, then drop down and lay prone in high grass or slight depressions, because they cannot outrun most predators when chased (Estes, 1967; Walther, 1969; Fitzgibbon, 1993b). Even adult antelopes exhibit this behavior. Some small bovid young are cached by their mothers in tall grass. Finding hidden calves is not easy and requires considerable time investment observing and evaluating mother and herd behavior. For example, cheetahs rarely succeed in ‘harvesting’ Thomson’s gazelle juveniles by searching for females or by relying on random encounters (Fitzgibbon, 1993a). Predators are more successful when they remain hidden from gazelle mothers and wait for them to reveal the juvenile’s location. For most African bovids nursing occurs 2–5 times a day and, in kudus and gazelles, is preceded by maternal vocalizations (Lent, 1974). This may provide regular opportunities for a predator to discover the locations of vulnerable nursing juveniles.

Modern carnivores including lions, spotted hyenas, and cheetahs are known to actively search for calves where antelope aggregate (e.g., Orsdol, 1984; Kruuk, 1972; Fitzgibbon, 1993a). Kanjera hominins may have exploited these small bovid behaviors and antipredator strategies to obtain the young gazelles that are so common in the mortality profile. If Kanjera hominins employed strategies such as those used by modern open-country predators to acquire prey, behaviors such as stalking and waiting to identify vulnerable individuals would be important skills.

The high frequency of small bovid juveniles at Kanjera is consistent with Expectation 1 and consonant with the possibility that hominins engaged in bouts of running while hunting. Whether this was persistence hunting as seen ethnographically in *Homo sapiens* (see Liebenberg, 2006) is difficult to determine, but it need not have involved long, sustained chases. Short chases to capture some small bovid juveniles seem likely.

5. Conclusions

Hominin entry into the carnivore guild about 2.6–1.8 Ma represents one of the most significant ecological, dietary, and behavioral shifts in our evolution. This study of Kanjera bovid mortality patterns and their comparison to those reported from FLK-Zinj (Bunn and Pickering, 2010a; Bunn and Gurtov, 2014) and samples created by extant carnivores suggests that Oldowan hominins at both locations acquired meat through hunting and scavenging, but because of different opportunities and constraints presented by the grassland and woodland habitats focused on different size bovids of different age classes.

Mortality and taphonomic data indicate that 2.0 Ma Kanjera hominins specialized in hunting vulnerable juveniles rather than relying upon chance encounters and scavenging of carnivore-kills. How Kanjera hominins may have hunted small bovids in an open habitat is speculative, but the mortality pattern is consistent with a conclusion that hunting involved short chases, at least occasionally. Notably, recent analysis of the only other Oldowan assemblage with an open habitat signature, the ca. 1.7 Ma HWK EE, indicates that small bovids were acquired with more meat than large bovids (Pante and de la Torre, 2017). The open grassland at Kanjera would offer little cover for hominins to regularly practice ambush hunting and acquire large bovids. Rather, the overabundance of large bovid heads indicates some scavenging of this size class. In contrast, as argued by Bunn and Gurtov (2014), the FLK-Zinj woodlands would provide cover facilitating ambush hunting. However, similarities between the FLK-Zinj, Olduvai Background, and lion mortality samples suggests that power scavenging occurred also. If interpretations of Kanjera South presented here and those for FLK Zinj by Bunn and Pickering (2010a) and Bunn and Gurtov (2014) are correct, then carcass acquisition strategies of Kanjera and FLK-Zinj hominins are almost mirror images of each other. Between 2.0 and 1.8 Ma, Oldowan hominins were habitually acquiring animals by both hunting and scavenging, the strategies for each being conditioned by habitat structure.

Acknowledgements

We are grateful to the Office of the President of Kenya, and the National Museums of Kenya for permission to study the Kanjera fossils and artifacts. The Homa Peninsula field research was conducted through the cooperative agreement between the National Museums of Kenya and the Smithsonian Institution. Funding from the L.S.B. Leakey Foundation, the National Geographic Society, the National Science Foundation, the Wenner-Gren Foundation, and the Professional Staff Congress-City University of New York Research Award Program for Kanjera field and laboratory work is gratefully acknowledged. The editor, D. Alba, reviewers, and Dwight Read (UCLA) provided insightful critiques that helped us substantially improve the paper. We thank Russ Graham and the Earth and Mineral Sciences Museum at Penn State University for their support. We thank Rick Potts and the Human Origins Program, Smithsonian Institution for support during all phases of the Kanjera research.

References

Aiello L.C., Wheeler P., 1995. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. Current Anthropology 36, 199–221.

Aiello, L.C., Wells, J.C.K., 2002. Energetics and the evolution of the genus *Homo*. Annual Review of Anthropology 31, 323–338.

Arráiz, H., Barboni, D., Ashley, G.M., Mabulla, A., Baquedano, E., Domínguez-Rodrigo, M., 2017. The FLK Zinj paleolandscape: Reconstruction of a 1.84 Ma wooded habitat in the FLK Zinj-AMK-PTK-DS archaeological complex, Middle Bed I (Olduvai Gorge, Tanzania). Palaeogeography, Palaeoclimatology, Palaeoecology 488, 9-20.

Ashley, G.M., Barboni, D., Domínguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Diez-Martin, F., Barba, R., Baquedano, E., 2010a. A spring and wooded habitat at FLK-Zinj and their relevance to origins of human behavior. Quaternary Research 74, 304-314.

Ashley, G.M., Domínguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z., Baquedano, E., 2010b. Sedimentary geology and human origins: a fresh look at Olduvai Gorge, Tanzania. Journal of Sedimentary Research 80, 703-709.

Behrensmeyer, A.K., Potts, R., Plummer, T., Tauxe, L., Opdyke, N., Jorstad, T., 1995. The Pleistocene locality of Kanjera, western Kenya: stratigraphy, chronology and paleoenvironments. Journal of Human Evolution 29, 247-274.

Bertram, B.C.B., 1999. Leopard. In Macdonald, D.W. (Ed.), The Encyclopedia of Mammals. Andromeda Oxford Limited, Oxford, pp. 44–48.

Bigalke, R.C., 1970. Observations on springbok populations. Zoological Africana 5, 59-70.

Bishop, L.C., Plummer, T.W., Ferraro, J.V., Braun, D., Ditchfield, P.W., Hertel, F., Kingston, J.D., Potts, R., 2006. Recent research into Oldowan hominin activities at Kanjera South, western Kenya. African Archaeological Review 23, 31-40.

Blumenschine, R. J., 1986. Early Hominid Scavenging Opportunities: Implications of Carcass Availability in the Serengeti and Ngorongoro Ecosystems. British Archaeological Reports, Oxford.

Blumenschine, R.J., 1987. Characteristics of an early hominid scavenging niche [and comments and reply]. Current Anthropology 28, 383-407.

Blumenschine, R.J., 1995. Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. Journal of Human Evolution 29, 21-51.

Blumenschine, R.J., Peters, C.R., 1998. Archaeological predictions for hominid land use in the paleo-Olduvai Basin, Tanzania, during lowermost Bed II times. Journal of Human Evolution 34, 565-608.

Blumenschine, R.J., Prassack, K.A., Kreger, C.D., Pante, M.C., 2007. Carnivore tooth-marks, microbial bioerosion, and the invalidation of Domínguez-Rodrigo and Barba's (2006) test of Oldowan hominin scavenging behavior. Journal of Human Evolution 53, 420-426.

Blumenschine, R.J., Stanistreet, I.G., Njau, J.K., Bamford, M.K., Masao, F.T., Albert. R.M., Stollhofen, H., Andrews, P., Prassack, K.A., McHenry, L.J., Fernández-Jalvo, Y., Camilli, E.L., Ebert J.I., 2012. Environments and hominin activities across the FLK Peninsula during *Zinjanthropus* times (1.84 Ma), Olduvai Gorge, Tanzania. Journal of Human Evolution 63, 364-383.

Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. University of Chicago Press, Chicago.

Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of *Homo*. Nature 432, 345-352.

Brantingham, P.J., 1998. Hominid–carnivore coevolution and invasion of the predatory guild. Journal of Anthropological Archaeology 17, 327-353.

Braun, D.R., Rogers, M.J., Harris, J.W., Walker, S.J., 2008. Landscape-scale variation in hominin tool use- evidence from the developed Oldowan. Journal of Human Evolution, 55, 1053-1063.

Braun, D.R., Harris, J.W., Levin, N.E., McCoy, J.T., Herries, A.I., Bamford, M.K., Bishop, L.C., Richmond, B.G., Kibunjia, M., 2010. Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. Proceedings of the National Academy of Sciences USA 107, 10002-10007.

Brown, A.D., Zunino, G.E., 1990. Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. Folia Primatologica 54, 187-195.

Bunn, H.T., 1986. Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. Journal of Human Evolution 15, 673-690.

Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Pleistocene hominids at Olduvai Gorge, Tanzania. Current Anthropology 27, 431-452.

Bunn, H.T., Kroll, E.M., 1987. Reply to “On butchery by Olduvai hominids”. Current Anthropology 28, 95-98.

Bunn, H.T., Pickering, T.R., 2010a. Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running–hunting and passive scavenging by early Pleistocene hominins. Quaternary Research 74, 395-404.

Bunn, H.T., Pickering, T.R., 2010b. Methodological recommendations for ungulate mortality analyses in paleoanthropology. Quaternary Research 74, 388-394.

Bunn, H.T., Gurtov, A.N., 2014. Prey mortality profiles indicate that Early Pleistocene Homo at Olduvai was an ambush predator. Quaternary International 322, 44-53.

Caro, T.M., 1986. The functions of stotting in Thomson's gazelles- some tests of the predictions. Animal Behaviour, 34, 663-684.

Caro, T.M., 1995. Pursuit-deterrence revisited. Trends in Ecology and Evolution, 10, 500-503.

Dasmann, R.F., Mossman, A.S., 1962. Population studies of impala in southern Rhodesia. Journal of Mammalogy 43, 375-395.

Ditchfield P., Hicks J., Plummer T.W., Bishop L., Potts R., 1999. Current research on the Plio-Pleistocene deposits north of Homa Mountain, southwestern Kenya. Journal of Human Evolution 36, 123-150.

Ditchfield, P., Whitfield, E., Vincent, T., Plummer, T., Braun, D., Deino, A., Hertel, F., Oliver, J.S., Louys, J., Bishop, L.C., 2018. Geochronology and physical context of Oldowan site formation at Kanjera South, Kenya. Geological Magazine https://doi.org/10.1017/S0016756818000602.

Domínguez-Rodrigo, M., Barba, R., 2006. New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site. the carnivore-hominid-carnivore hypothesis falsified. Journal of Human Evolution 50, 170-194.

Domínguez-Rodrigo, M., Barba, R., Egeland, C.P. (Eds.), 2007. Deconstructing Olduvai: A Taphonomic Study of the Bed I Sites. Springer, New York.

Domínguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Ashley, G.M., Diez-Martin, F., Barboni, D., Prendergast. M.E., Yravedra, J., Barba, R., Sánchez, A. Baquedano. E., Pickering, T.R., 2010. New excavations at the FLK *Zinjanthropus* site and its surrounding landscape and their behavioral implications. Quaternary Research 74, 315-332.

Domínguez-Rodrigo, M., Bunn, H.T., Yravedra, J., 2014. A critical re-evaluation of bone surface modification models for inferring fossil hominin and carnivore interactions through a multivariate approach: application to the FLK Zinj archaeofaunal assemblage (Olduvai Gorge, Tanzania). Quaternary International 322, 32-43.

Domínguez-Rodrigo, M., Baquedano, E., Mabulla, A.Z.P., Mercader. J., Egeland, C.P., 2017. Paleoecological reconstructions of the Bed I and Bed II lacustrine basins of Olduvai Gorge (Tanzania) and insights into early human behavior. Palaeogeography, Palaeoclimatology, Palaeoecology 488, 1-8.

Elliott, J.P., Cowan, I.M., Holling, C.S., 1977. Prey capture by the African lion. Canadian Journal of Zoology 55, 1811-1828.

Endler, J.A., 1986. Defense against predators. In: Federand, M.E., Lauder, G.V. (Eds.), Predator-Prey Relationships: Perspective and Approaches from the Study of Lower Vertebrates. University of Chicago Press, Chicago, pp. 109–134.

Estes, R.D., 1967. The comparative behaviour of Grant's and Thomson's gazelles. Journal of Mammalogy 48, 189-209.

Estes, R.D., 1974. Social organization of the African Bovidae. In: Geist, V., Walther, F. (Eds.), The Behaviour of Ungulates and Its Relation to Management, 1. International Union for Conservation of Nature and Natural Resources, Switzerland, pp. 166-205.

Estes, R., 1991. The Behavior Guide to African Mammals. University of California Press, Berkeley.

Faith, J.T., Domínguez-Rodrigo, M., Gordon, A.D., 2009. Long-distance carcass transport at Olduvai Gorge? A quantitative examination of Bed I skeletal element abundances. Journal of Human Evolution 56, 247-256.

Ferraro, J.V., 2007. Broken bones and shattered stones: on the foraging ecology of Oldowan hominins. Ph.D. Dissertation, University of California, Los Angeles.

Ferraro, J.V., Plummer, T.W., Pobiner, B.L., Oliver, J.S., Bishop, L.C., Braun, D.R., Ditchfield, P.W., Seaman III, J.W., Binetti, K.M., Seaman, J.W. Jr., Hertel, F., 2013. Earliest archaeological evidence of persistent hominin carnivory. PLoS One 8, e62174.

Fitzgibbon, C.D., 1990. Anti-predator strategies of immature Thomson's gazelles: hiding and the prone response. Animal Behaviour, 40, 846-855.

FitzGibbon, C.D., 1993a. Antipredator strategies of female Thomson's gazelles with hidden fawns. Journal of Mammalogy 74, 758-762.

Fitzgibbon, C.D., 1993b. Cheetahs and gazelles: A study of individual variation in antipredator behaviour and predation risk. Physiology and Ecology Japan 29, 195-206.

FitzGibbon, C.D., Fanshawe, J. H., 1988. Stotting in Thomson's gazelles- an honest signal of condition. Behavioral Ecology and Sociobiology 23, 69-74.

Foley, R., 1987. Another Unique Species: Patterns in Human Evolutionary Ecology. Longman Science and Technology, London.

Foley, R., 2001. The evolutionary consequences of increased carnivory in hominids. In: Stanford, C.B., Bunn, H.T., (Eds.), Meat-Eating and Human Evolution. Oxford University Press, Oxford, pp. 305–331.

Ganas, J., Robbins, M. M., Nkurunungi, J. B., Kaplin, B. A., McNeilage, A., 2004. Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. International Journal of Primatology 25, 1043-1072.

Gentry, A.W., Gentry, A., 1978. Fossil Bovidae (Mammalia) of Olduvai Gorge*,* Tanzania. Part I. Bulletin of the British Museum (Natural History): Geology 29, 289-446.

Grine, F.E., Fleagle, J.G., Leakey, R. E. (Eds.). 2009. The First Humans: Origin and Early Evolution of the Genus *Homo*. Springer, New York.

Gros, P.M., Rejmánek, M. (1999). Status and habitat preferences of Uganda cheetahs- an attempt to predict carnivore occurrence based on vegetation structure. Biodiversity and Conservation 8, 1561-1583.

Hay, R.L., 1973. Lithofacies and environments of Bed I, Olduvai Gorge, Tanzania.Quaternary Research 3, 541-560.

Hayward, M.W., Henschel, P., O'brien, J., Hofmeyr, M., Balme, G., Kerley, G.I.H., 2006. Prey preferences of the leopard (*Panthera pardus*). Journal of Zoology, 270, 98-313.

Hill, R.A., Dunbar, R.I.M., 2002. Climatic determinants of diet and foraging behaviour in baboons. Evolutionary Ecology 16, 579-593.

Hirst, S.M., 1969. Populations in a Transvaal lowveld nature reserve. Zoologica Africana 4, 199-230.

Hopcraft, J.G.C., Sinclair, A.R.E., Packer, C., 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology, 74, 559-566.

Jackson, C.R., Power, R.J., Groom, R.J., Masenga, E.H., Mjingo, E.E., Fyumagwa, R. D., Røskaf, E., Davies-Mostert, H., 2014. Heading for the hills: risk avoidance drives den site selection in African wild dogs. PLoS One, 9, e99686.

Jaeger, J.J., 1976. Les rongeurs (mammalia, Rodentia) du Pleistocene inferieur d'Olduvai Bed I (Tanzanie), 1ere partie : Les Muridés. In: Savage, R.J.G., Coryndon, S.C. (Eds.), Fossil Vertebrates of Africa. Academic Press, London, pp. 57-120.

Klein, R.G., 1976. The mammalian fauna of the Klasies River mouth sites, southern Cape Province, South Africa. The South African Archaeological Bulletin, 31, 75-98.

Klein, R.G., 1978. Stone Age predation on large African bovids. Journal of Archaeological Science 5, 195-217.

Klein, R.G., 1982. Patterns of ungulate mortality and ungulate mortality profiles from

Langebaanweg (Early Pliocene) and Elandsfontein (Middle Pleistocene), south-western Cape Province, South Africa. Annals of the South African Museum, 90, 49-64.

Kroll, E.M., Isaac, G.L., 1984. Configurations of artifacts and bones at early Pleistocene sites in East Africa. In: Hietala, H. (Ed.), Intrasite Spatial Analysis in Archaeology. Cambridge University Press, Cambridge, pp. 4-31.

Kruuk, H., 1972. The Spotted Hyena. University of Chicago Press, Chicago.

Leakey M.D., 1971. Olduvai Gorge: Excavations in Beds I and II, 1960–1963. Cambridge University Press, Cambridge.

Lent, P.C., 1974. Mother-infant relationships in ungulates. In: Geist, V., Walther, F., (Eds.), The Behaviour of Ungulates and Its Relation to Management, 1. International Union for Conservation and Natural Resources Publications, Morges, pp. 14-55.

Lewis, M.E., Werdelin, L., 2007. Patterns of change in the Plio-Pleistocene carnivorans of eastern Africa. In: Bobe, R., Alemseged, Z., Behrensmeyer, A.K. (Eds.), Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence. Springer, Dordrecht, pp. 77-105.

Liebenberg, L., 2006. Persistence hunting by modern hunter-gatherers. Current Anthropolology 47, 1017-1026.

Lieberman, D.E., Bramble, D.M., Raichlen, D.A., Shea, J.J., 2007. The evolution of endurance running and the tyranny of ethnography: a reply to Pickering and Bunn. Journal of Human Evolution 53, 434-437.

Lordkipanidze, D., Ponce de León, M.S., Margvelashvili, A., Rak, Y., Rightmire, G.P., Vekua, A., Zollikofer, C.P., 2013. A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*. Science, 342, 326-331.

Magill, C.R., Ashley, G.M., Domínguez-Rodrigo, M., Freeman, K.H., 2016. Dietary options and behavior suggested by plant biomarker evidence in an early human habitat. Proceedings of the National Academy of Sciences USA 113, 2874-2879.

McCoy, E.D., Bell, S.S., 1991. Habitat structure: the evolution and diversification of a complex topic. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R., (Eds.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall, New York, pp. 3-27.

Mitchell, B.L., Shenton, J.B., Uys, J.C.M., 1965. Predation on large mammals in the Kafue National Park, Zambia. Zoological Africana 1, 297-318.

Moore, J., Black, J., Hernandez-Aguilar, R. A., Idani, G. I., Piel, A., Stewart, F. 2017. Chimpanzee vertebrate consumption- Savanna and forest chimpanzees compared. Journal of Human Evolution 112, 30-40.

Ndibalema, V.G., 2009. A comparison of sex ratio, birth periods and calf survival among Serengeti wildebeest sub-populations, Tanzania. African Journal of Ecology 47, 574-582.

Oliver, J.S., 1994. Estimates of hominid and carnivore involvement in the FLK-*Zinjanthropus* fossil assemblage: Some socioecological implications. In Oliver, J.S., Sikes, N.E., Stewart, K.M. (Eds.), Early Hominid Behavioral Ecology. Journal of Human Evolution 27, 267-294.

Oliver, J.S., 2015. Diagnosing bone fracture to assess early hominin behaviour, meat-eating, and socioecology at FLK-*Zinjanthropus*, Olduvai Gorge, Tanzania. Ph.D. Dissertation, Liverpool John Moores University.

Orsdol, K.G., 1984. Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. African Journal of Ecology 22, 79-99.

Owen-Smith, N., 2006. Demographic determination of the shape of density dependence for three African ungulate populations. Ecological Monographs 76, 93-109.

Pante, M.C., Blumenschine, R.J., Capaldo, S.D., Scott, R.S., 2012. Validation of bone surface modification models for inferring fossil hominin and carnivore feeding interactions, with reapplication to FLK 22, Olduvai Gorge, Tanzania. Journal of Human Evolution 63, 395-407.

Pante, M.C., Scott, R.S., Blumenschine, R.J., Capaldo, S.D., 2015. Revalidation of bone surface modification models for inferring fossil hominin and carnivore feeding interactions. Quaternary International 355, 164-168.

Pante, M.C., de la Torre, I., 2017. A hidden treasure of the Lower Pleistocene at Olduvai Gorge, Tanzania: The Leakey HWK EE assemblage. Journal of Human Evolution 120, 114-139.

Parkinson, J.A., 2013. A GIS Image analysis approach to documenting Oldowan hominin carcass acquisition: evidence from Kanjera South, FLK Zinj, and neotaphonomic models of carnivore bone destruction. Ph.D. Dissertation, City University of New York.

Parkinson, J.A., Plummer, T., Hartstone-Rose, A., 2015. Characterizing felid tooth marking and gross bone damage patterns using GIS image analysis: an experimental feeding study with large felids. Journal of Human Evolution 80, 114-134.

Peters, C.R., Blumenschine, R.J., 1995. Landscape perspectives on possible land use patterns for Early Pleistocene hominids in the Olduvai Basin, Tanzania. Journal of Human Evolution 29, 321-362.

Plummer, T., 2004. Flaked stones and old bones: biological and cultural evolution at the dawn of technology. American Journal of Physical Anthropology 125, 118-164.

Plummer, T.W., Bishop, L.C., 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. In: Oliver, J.S., Sikes, N.E. Stewart, K.M. (Eds.), Early Hominid Behavioral Ecology. Journal of Human Evolution 27, 47-75.

Plummer, T.W., Bishop, L., Ditchfield, P., Hicks, J., 1999. Research on Late Pliocene Oldowan sites at Kanjera South, Kenya. Journal of Human Evolution 36, 151-170.

Plummer, T.W., Ditchfield, P.W., Bishop, L.C., Kingston, J.D., Ferraro, J.V., Braun, D. R., Hertel, F., Potts, R., 2009a. Oldest evidence of toolmaking hominins in a grassland-dominated ecosystem. PLoS One 4, e7199.

Plummer, T.W., Bishop, L.C., Ditchfield, P.W., Ferraro, J.V., Kingston, J.D., Hertel, F., Braun, D.R., 2009b. The environmental context of Oldowan hominin activities at Kanjera South, Kenya. In: Hovers, E., Braun, D.R. (Eds.), Interdisciplinary Approaches to the Oldowan. Springer, Dordrecht, pp. 149-160.

Potts R., 1986. Temporal span of bone accumulations at Olduvai Gorge and implications for early hominid foraging behavior. Paleobiology 12, 25-31.

Potts, R., 1987. On butchery by Olduvai hominids. Current Anthropology 28, 95-98.

Potts R., 1988. Early Hominid Activities at Olduvai. Aldine De Gruyter, New York.

Riney, T., Child, G., 1960. Breeding season and ageing criteria for the common duiker (*Sylvicapra grimmia*). Proceedings of the Federal Science Congress 1, 291-299.

Robinette, W.L., Archer, A.L., 1971. Notes on ageing criteria and reproduction of Thomson's gazelle. African Journal of Ecology 9, 83-98.

Schaller, G.B., 1968. Hunting behaviour of the cheetah in the Serengeti National Park, Tanzania. African Journal of Ecology, 6, 95-100.

Schaller, G.B., 1972. The Serengeti Lion. University of Chicago Press, Chicago.

Tooby, J., 1987. Characteristics of an early hominid scavenging niche. Comments. Current Anthropology 28, 399-400.

Toth, N.P., Schick, K.D. (Eds.), 2006. The Oldowan: Case Studies Into the Earliest Stone Age. Stone Age Institute Press, Gosport.

Trapp, J.R., Beier, P., Mack, C., Parsons, D.R., Paquet, P.C., 2008. Wolf, *Canis lupus*, den site selection in the Rocky Mountains. The Canadian Field-Naturalist 122, 49-56.

Sikes, N.E., 1994. Early hominid habitat preferences in East Africa: paleosol carbon isotopic evidence. In: Oliver, J.S., Sikes, N.E. Stewart, K.M. (Eds.), Early Hominid Behavioral Ecology. Journal of Human Evolution *27*, 25-45.

Spinage, C.A., 1967. Ageing the Uganda defassa waterbuck *Kobus defassa ugandae* Neumann. African Journal of Ecology 5, 1-17.

Spinage, C.A., 1971. Geratodontology and horn growth of the impala (*Aepyceros melampus*). Journal of Zoology 164, 209-225.

Spinage, C.A., 1972. African ungulate life tables. Ecology 53, 645-652

Spinage, C.A., 1982. A Territorial Antelope: The Uganda Waterbuck. Academic Press, London.

Stander, P.E., 1992. Foraging dynamics of lions in a semi-arid environment. Canadian Journal of Zoology 70, 8-21.

Steele, T.E., Weaver, T.D., 2002. The modified triangular graph: a refined method for comparing mortality profiles in archaeological samples. Journal of Archaeological Science 29, 317-322.

Stephens, P.W., Peterson, R.O., 1984. Wolf-avoidance strategies of moose. Holarctic Ecology 7, 239-244.

Stiner, M.C., 1990. The use of mortality patterns in archaeological studies of hominid predatory adaptations. Journal of Anthropological Archaeolology 9, 305-351.

Talbot, L.M., Talbot, M.H., 1963. The wildebeest in western Masailand, East Africa. Wildlife Monographs 12, 3-88.

Tappen, M., 1995. Savanna ecology and natural bone deposition- implications for early hominid site formation, hunting, and scavenging. Current Anthropology 36, 223-260.

Theuerkauf, J., Rouys, S., Jedrzejewski, W., 2003. Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. Canadian Journal of Zoology, 81, 163-167.

Tooby, J., 1987. Reply to Blumensching, R., Characteristics of an early hominid scavenging niche [and comments and reply]. Current Anthropology 28, 383-407.

Underwood, R., 1975. Social Behaviour of the Eland (*Taurotragus oryx*) on Loskop Dam Nature Reserve. MSc Thesis, University of Pretoria.

Walther, F.R., 1969. Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). Behaviour, 34, 184-220.

Weaver, T.D., Boyko, R.H., Steele, T.E., 2011. Cross-platform program for likelihood-based statistical comparisons of mortality profiles on a triangular graph. Journal of Archaeological Science 38, 2420-2423

Werdelin, L., Lewis, M.E., 2013. Temporal change in functional richness and evenness in the eastern African Plio-Pleistocene carnivoran guild. PLoS One 8, e57944.

Whittaker, R., 1975. Communities and Ecosystems. Macmillan, New York.

Wilson, D.E., Mittermeier, R.A., 2009. Handbook of Mammals of the World. Vol. 1 Carnivores. Lynx Edicions, Barcelona.

Zhu, Z., Dennell, R., Huang, W., Wu, Y., Qiu, S., Yang, S., Rao, Z., Hou, Y., Xie, J., Han, J. and Ouyang, T., 2018. Hominin occupation of the Chinese Loess Plateau since about 2.1 million years ago. Nature 559, 608-612.

Figure 1. Ternary diagram showing the major mortality patterns defined by Stiner (1990). Attritional mortality samples are characterized by preponderance of juveniles, a lower frequency of prime adults and to a lesser degree old adults due to the greater susceptibility of juveniles and old adults to succumb to disease, predation, accidents, and poor nutrition compared to prime adults. The attritional zone corresponds to the u-shaped profiles created when an age distribution is plotted in a histogram. The living structure mortality pattern is characterized by a preponderance of prime adults and many fewer juveniles and old adults, as is the case with standing populations. Because ambush carnivores lie in wait, they tend to sample age groups in proportion to their frequency in the standing population and therefore create mortality samples with high frequencies of prime adults that plot within the living structure zone. Cursorial carnivores, however, exploit prey vulnerabilities and consequently tend to create mortality samples dominated by juveniles that plot within the attritional structure zone of the ternary diagram. As noted by Stiner (1990) extant carnivores rarely create prime-dominated assemblages, but human hunters with effective killing technologies may often do so.

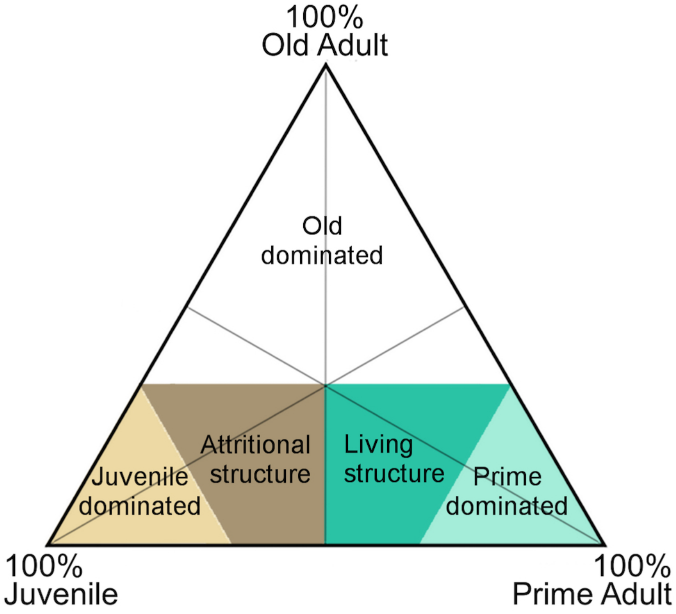
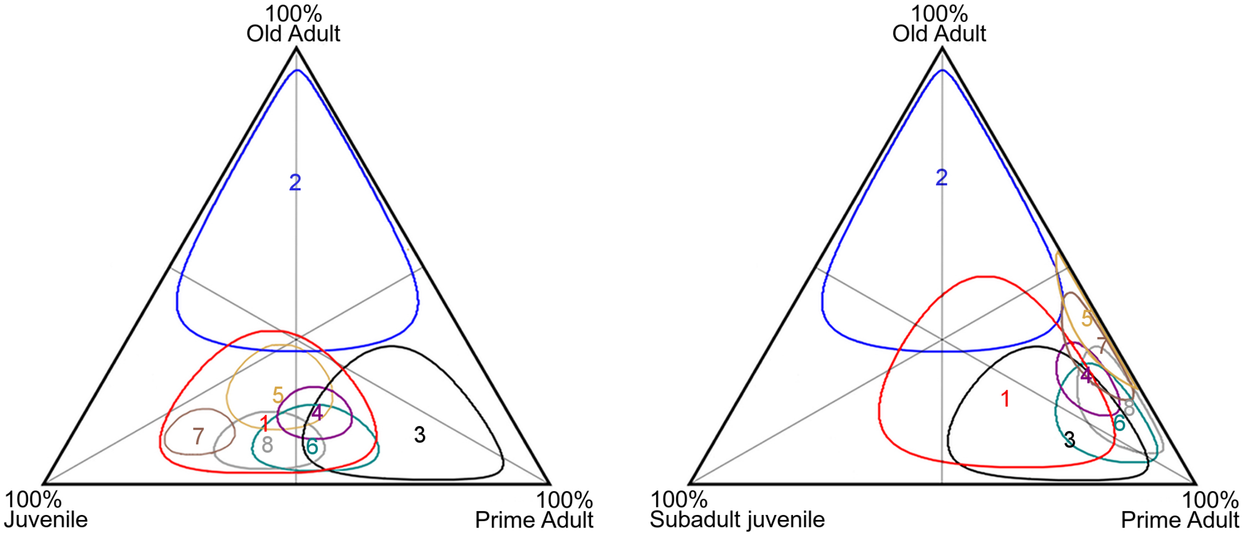
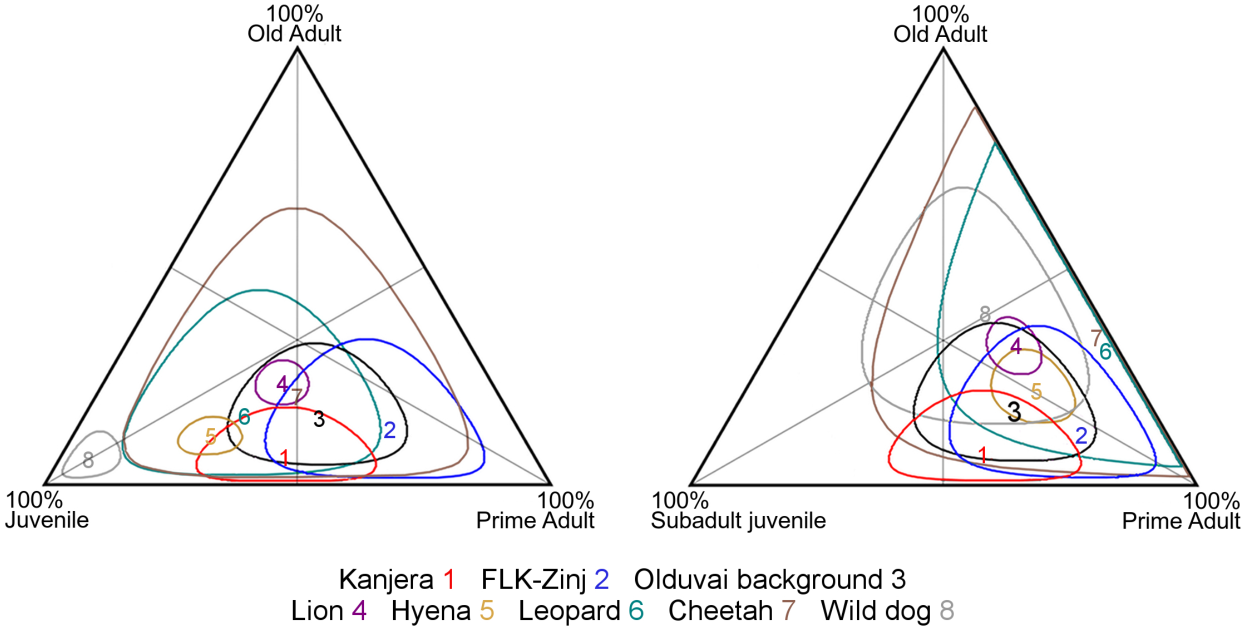


Figure 2. Modified triangle graphs showing mortality pattern for small (a, b) and large (c, d) bovids killed by lions, hyenas, leopards, cheetahs, and wild dogs, and those for Kanjera, FLK-Zinj, and the Olduvai Background that include (a, c) and exclude (b, d) young juveniles. Colored ellipses approximate the 95% confidence intervals (CI) of each sample. The numbered data points of the same color represent the percentage values of juvenile, prime-adult, and old individuals in each sample (the age proportions value). Carnivore-kill data are totals from Table 3 and associated citations. Mortality data for Kanjera, FLK-Zinj, and Olduvai background are from Table 2.



a) Small bovid: all juveniles

b) Small bovid: no young juveniles

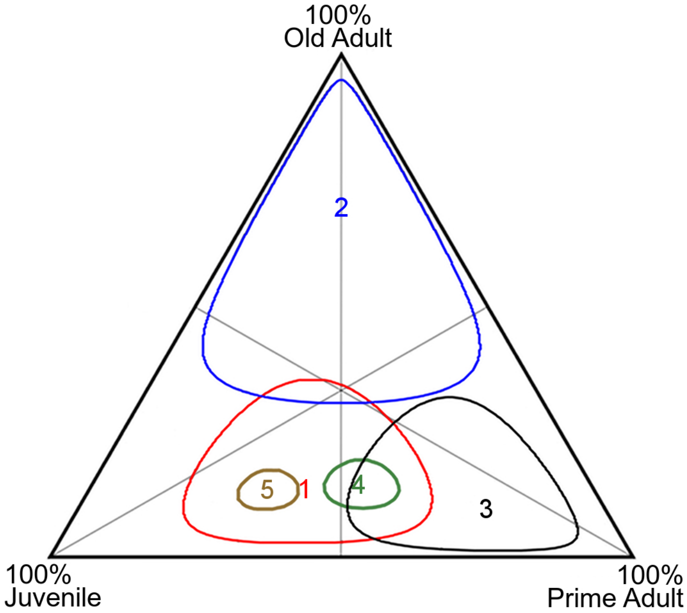


c) Large bovid: all juveniles

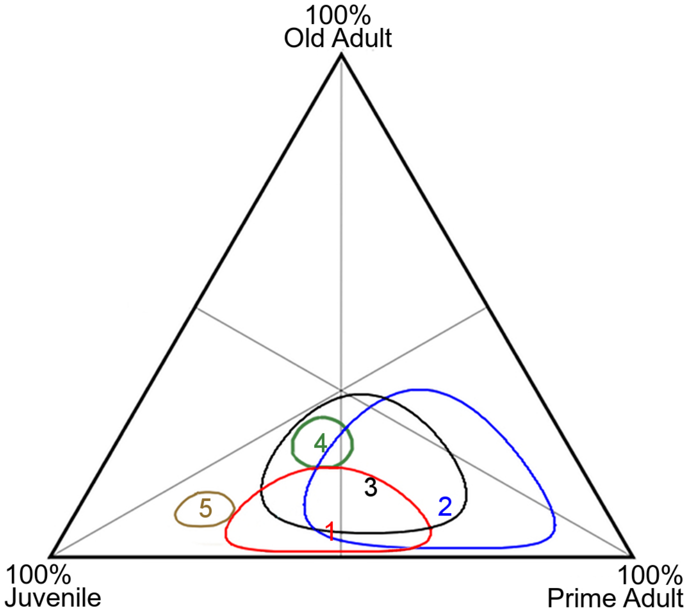
d) Large bovid: no young juveniles

Figure 3. Modified triangle graphs showing small (a) and large (b) bovid mortality patterns for the pooled sample of bovids killed by ambush (lions and leopards) and cursorial (hyenas, cheetahs, and wild dogs) predators and those for the Kanjera, FLK-Zinj, and Olduvai Background bovid assemblages. Colored ellipses approximate the 95% confidence intervals (CI) of each sample. The numbered data points of the same color represent the percentage value of juvenile, prime-adult, and old individuals in each sample (the age proportions value). Pooled carnivore kill data are totals from Table 3, derived from the data in the associated citations. Mortality data for Kanjera, FLK-Zinj, and the Olduvai background are from Table 2.

a) Ambush vs. cursorial predators: small bovids



b) Ambush vs. cursorial predators: large bovids



Kanjera 1 FLK-Zinj 2 Olduvai background 3
Ambush predator 4 Cursorial predator 5

Table 1
Age categories for small (size class 1–2) and large (size class 3) bovids as defined by the cheek teeth eruption and wear described in the wildlife literature.[a]

Age class	Size class	Tooth eruption and wear
Young juvenile	1–3	Light to moderately worn deciduous premolars; erupted or erupting M_1, M_2, and M^1; M^2 erupted in small bovids
Subadult juvenile	1–3	Moderately to heavily worn or shed deciduous premolars; erupting or erupted P_3–P_4 and M_1–M_3; late eruption and wear of M^{2-3} large bovids
Early prime	1–2	Permanent dentition moderately worn; smaller bovids display rapid, early loss of the mesial infundibulum of M_1 within the early prime adult class; all permanent teeth in maxilla in use with near loss of M^1 mesial infundibula
	2?–3	All permanent dentition present; light to moderate to heavy occlusal wear; no infundibulum loss
Late prime	1–2	Substantial wear on full permanent dentition; loss of M_1 mesial and extensive wear or loss of distal infundibula; loss of M^1 mesial infundibula; P^{3-4} and M^{2-3} heavily worn
	3	Moderate to substantial occlusal wear; no loss of mesial M_1 infundibulum
Old	1–3	Heavy occlusal wear and loss of both mesial and distal infundibula on M_1 and M_2; M^{1-3} infundibula absent or heavily worn

[a] Age estimates for size 1–2 bovids were based on tooth eruption and infundibula wear schemes for a) Thomson's gazelle (*Eudorcas thomsonii*), described by Schaller (1972:Table 48), Kruuk (1972: Appendix D7), and Robinette and Archer (1971); b) impala (*Aepyceros melampus*), reported by Spinage (1971); c) common duiker (*Sylvicapra grimmia*), described by Riney and Child (1960); and d) small bovids, given by Mitchell et al. (1965). Age estimates for size 3 bovids followed tooth eruption and infundibula wear schemes for a) wildebeest (*Connochaetes taurinus*), described by Kruuk (1972:Appendix D7), Schaller (1972:Table 44), and Talbot and Talbot (1963:Fig. 9); b) waterbuck (*Kobus ellipsiprymnus*), given by Spinage (1967:Appendix D7); and c) size 3 bovids, given by Mitchell et al. (1965) and Spinage (1982).

Table 2

Age frequencies (minimum number of individuals, MNI) of bovid dentognathic remains from Kanjera South Beds 1–3, Homa Peninsula, Kenya and those reported by Bunn and Pickering (2010b:Table 1) for the FLK-Zinj and Background assemblages, Olduvai Gorge, Tanzania. Kanjera Bed 2CP/3CP, formed by water flow, is not included.[a]

	Juvenile MNI			Adult MNI		Total MNI	
Sample	Young	Subadult	Total juvenile	Prime adult	Old adult	Including young juvenile	Excluding young juvenile
Kanjera small bovid							
Antelopini (1)	5	2	7	5	3	15	10
Bovidae (1)	0	1	1	2	0	3	3
Bovidae (2)	2	1	3	1	0	4	2
Kanjera small bovid total	7	4	11	8	3	22	15
Kanjera large bovid							
Alcelaphini (3a)	3	8	11	14	0	25	22
Alcelaphini (3b)	0	1	1	0	1	2	2
Reduncini (3a)	1	1	2	1	1	4	3
Bovidae (3a)	3	1	4	1	0	5	2
Bovidae (3b)	1	1	2	2	0	4	3
Kanjera large bovid total	8	12	20	18	2	40	32
Total Kanjera bovid	15	16	31	26	5	62	47
FLK-Zinj small bovid							
Antidorcas recki (1)	0	1	1	1	4	6	6
Antelopini (1)	0	0	0	0	1	1	1
FLJ-Zinj small bovid total	0	1	1	1	5	7	7
FLK-Zinj large bovid							
Parmularius altidens (3a)	0	3	3	2	1	6	6
Connochaetes sp. (3b)	0	0	0	3	0	3	3
Kobus sigmoidalis (3b)	2	0	2	7	0	9	7
Oryx sp. (3b)	0	0	0	0	1	1	1
FLJ-Zinj large bovid total	2	3	5	12	2	19	17
Total FLJ-Zinj bovid	2	4	6	13	7	26	24
‘Background’ small bovid							
FLK-N 1-2	0	3	3	10	1	14	14
FLK-N 6	0	1	1	4	1	6	6
‘Background’ small bovid total	0	4	4	14	2	20	20
‘Background’ large bovid							
FLK-N 1-2	2	3	5	7	1	13	11
FLK-N 6	1	3	4	5	3	12	11
FLK-NN 2	2	2	4	4	1	9	7
‘Background’ large bovid total	5	8	13	16	5	34	29
Total ‘Background’ bovid	5	12	17	30	7	54	49

[a] Age categories follow Bunn and Pickering (2010a, b; see Table 1 for teeth eruption and wear characters used to age dentognathic specimens). Bovid size groups (indicated by number in parentheses) follow Bunn (1986).

Table 3
Age frequencies (minimum number of individuals, MNI) of bovids killed by modern carnivores. Age categories follow Bunn and Pickering (2010a,b). Bovid size groups follow Bunn (1986).

	Juvenile MNI			Adult MNI		Total MNI	
Sample	Young	Subadult	Total juvenile	Prime adult	Old	Including young juvenile	Excluding young juvenile
Serengeti carnivore-killed small bovid							
Lion-killed *Eudorcas thomsonii* [a]	67	12	79	93	32	204	137
Hyena-killed *Eudorcas thomsonii* [b]	42	0	42	35	21	98	56
Leopard-killed *Eudorcas thomsonii* [c]	9	4	13	15	2	30	21
Cheetah-killed *Eudorcas thomsonii* [c]	124	2	126	44	22	192	68
Wild dog-killed *Eudorcas thomsonii* [d]	34	2	36	21	8	65	31
Total Serengeti small bovid	276	20	296	208	85	589	313
Kafue lion-killed small bovid							
Aepyceros melampus [e]	2	0	2	2	0	4	2
Kobus vardonii [e]	1	0	1	0	1	2	1
Redunca arundinum [e]	0	0	0	1	0	1	1
Tragelaphus sp. [e]	0	0	0	0	1	1	1
Kobus leche [e]	0	0	0	1	0	1	1
Kafue lion-killed small bovid	3	0	3	4	2	9	6
Kafue leopard-killed small bovid							
Sylvicapra grimmia [f]	5	0	5	5	0	10	5
Raphicerus melanotis [f]	1	0	1	3	0	4	3
Ourebia ourebi [f]	1	0	1	1	0	2	1
Aepyceros melampus [f]	3	0	3	2	2	7	4
Kobus vardonii [f]	4	0	4	6	2	12	8
Redunca arundinum [f]	6	0	6	3	1	10	4
Tragelaphus sp. [f]	0	0	0	3	0	3	3
Kobus leche [f]	0	0	0	1	0	1	1
Kafue leopard-killed small bovid	20	0	20	24	5	49	29

Kafue Cheetah-killed small bovid							
Ourebia ourebi [g]	1	0	1	0	0	1	0
Aepyceros melampus [g]	1	0	1	0	0	1	0
Kobus vardonii [g]	4	0	4	6	2	12	8
Redunca arundinum [g]	2	0	2	1	0	3	1
Kafue cheetah-killed small bovid	8	0	8	7	2	17	9
Kafue wild dog-killed small bovid							
Sylvicapra grimmia [h]	9	0	9	6	1	16	7
Ourebia ourebi [h]	0	0	0	1	0	1	1
Kobus vardonii [h]	0	0	0	3	0	3	3
Redunca arundinum [h]	11	0	11	6	0	17	6
Tragelaphus sp. [h]	0	0	0	4	0	4	4
Kobus leche [h]	1	0	1	0	0	1	0
Kafue wild dog-killed small bovid	21	0	21	20	1	42	21
Total Kafue small bovid	52	0	52	55	10	117	65
Serengeti carnivore-killed large bovid							
Lion-killed *Connochaetes taurinus* [i]	72	50	122	78	62	262	190
Hyena-killed *Connochaetes taurinus* [j]	31	14	45	17	24	86	55
Wild dog-killed *Connochaetes taurinus* [d]	72	2	74	0	0	74	2
Total Serengeti large bovid	175	66	241	95	86	422	247
Ngorogoro carnivore-killed large bovid							
Spotted Hyena-killed *C. taurinus* [j]	115	13	128	59	4	191	76
Total Ngorogoro large bovid	115	13	128	59	4	191	76
Rwenzori carnivore-killed large bovid							
Lion-killed *Kobus ellipsiprymnus* [k]	0	2	2	4	3	9	9
Total Rwenzori large bovid	0	2	2	4	3	9	9
Kafue lion-killed large bovid							
Alcelaphus buselaphus [e]	15	2	17	26	8	51	36
Tragelaphus strepsiceros [e]	0	0	0	1	1	2	2
Hippotragus equinus [e]	4	0	4	6	7	17	13

Hippotragus niger[e]	5	1	6	8	2	16	11
Kobus ellipsiprymnus[e]	4	0	4	6	3	13	9
Connochaetes taurinus[e]	5	1	6	8	3	17	12
Kafue lion-killed large bovid	33	4	37	55	24	116	83
Kafue leopard-killed large bovid							
Alcelaphus buselaphus[f]	4	0	4	4	1	9	5
Tragelaphus strepsiceros[f]	2	0	2	0	1	3	1
Connochaetes taurinus[f]	1	0	1	0	0	1	0
Kafue leopard-killed large bovid	7	0	7	4	2	13	6
Kafue cheetah-killed large bovid							
Alcelaphus buselaphus[g]	1	0	1	1	1	3	2
Tragelaphus strepsiceros[g]	0	0	0	1	0	1	1
Connochaetes taurinus[g]	1	0	1	0	0	1	0
Kafue cheetah-killed large bovid	2	0	2	2	1	5	3
Kafue wild dog-killed large bovid							
Alcelaphus buselaphus[h]	9	1	10	1	3	14	5
Tragelaphus strepsiceros[h]	1	0	1	2	1	4	3
Hippotragus equinus[h]	0	0	0	0	0	0	0
Hippotragus niger[h]	2	0	2	1	1	4	2
Kobus ellipsiprymnus[h]	1	0	1	1	0	2	1
Connochaetes taurinus[h]	2	0	2	0	0	2	0
Kafue wild dog-killed large bovid	15	1	16	5	5	26	11
Total Kafue large bovid	57	5	62	66	14	142	85
Total small bovid							
Lion-killed	70	12	82	97	34	213	143
Leopard-killed	29	4	33	39	7	79	50
Ambush total	99	16	115	136	43	292	193
Spotted hyena-killed	42	0	42	35	21	98	56
Cheetah-killed	132	2	134	51	24	209	77
Wild dog-killed	55	2	57	41	9	107	52
Cursorial total	229	4	233	127	54	414	185

Total small bovid	328	20	348	263	95	706	378
Total large bovid							
Lion-killed	105	56	161	137	89	387	282
Leopard-killed	7	0	7	4	2	13	6
Ambush total	112	56	168	141	91	400	288
Spotted hyena-killed	146	27	173	76	28	277	131
Cheetah-killed	2	0	2	2	1	5	3
Wild dog-killed	87	3	90	5	5	100	13
Cursorial total	135	30	265	83	34	382	147
Total large bovid	347	86	433	224	125	782	435

[a] Schaller (1972:Table 49).
[b] Kruuk (1972:Fig. 25).
[c] Schaller (1972:Table 64).
[d] Schaller (1972:Table 67).
[e] Mitchell et al. (1965:Table 10).
[f] Mitchell et al. (1965:Table 11).
[g] Mitchell et al. (1965:Table 12).
i Mitchell et al., (1965:Table 13).
[i] Schaller (1972:Table 45).
[j] Kruuk (1972:Fig. 23).
[k] Spinage (1982:156).

Table 4
Age frequency distributions (% minimum number of individuals, MNI) of modern African bovid populations.

Sample	Juvenile	1 year to subadult	Total juvenile	Prime adult	Old	Total adult
Small bovid						
Aepyceros melampus: Akagera National Park [a]	18.7	12.9	31.7	nd	nd	68.3
Aepyceros melampus: Akagera National Park [b]	23.6	15.4	39.1	nd	nd	61.0
Akagera National Park *A. melampus* average	21.2	14.2	35.4	nd	nd	64.6
Aepyceros melampus: Rhodesia (Zimbabwe) [c]	28.5	15.9	44.4	nd	nd	55.6
Large bovid						
Taurotragus oryx, South Africa [d]	nd	nd	41.9	57.0	1.1	58.1
Syncerus caffer: Akagera National Park [e]	18.9	18.3	37.2	54.4	8.4	62.8
Tragelaphus strepsiceros: Kruger National Park [f]	18.8	17.5	36.5	43.6	20.1	63.7
Tragelaphus strepsiceros: Timbavati Reserve (1964) [g]	9.1	14.9	23.9	nd	nd	76.1
Tragelaphus strepsiceros: Timbavati Reserve (1965) [g]	12.9	15.4	28.3	nd	nd	71.7
Tragelaphus strepsiceros: Timbavati Reserve (1967) [g]	16.9	10.6	27.5	nd	nd	72.5
Timbavati Reserve *T. strepsiceros* average	13.0	13.6	26.6	nd	nd	73.4
Connochaetes taurinus: Kruger National Park [h]	19.4	11.9	31.3	nd	nd	68.7
Connochaetes taurinus: Timbavati Reserve (1965) [i]	20.8	11.9	32.7	nd	nd	67.3
Connochaetes taurinus: Timbavati Reserve (1966) [i]	18.8	10.4	29.2	nd	nd	70.8
Connochaetea taurinus: Timbavati Reserve (1967) [i]	28.1	13.7	41.8	nd	nd	58.2
Timbavati *C. taurinus* average	22.6	12.0	34.6	nd	nd	65.4
Connochaetes taurinus: Serengeti resident [j]	27.9	13.5	41.4	nd	nd	58.6
Connochaetes taurinus: Serengeti migratory [j]	19.2	15.0	34.2	nd	nd	65.8
Connochaetes taurinus: Serengeti [k]	15.8	24.6	40.4	51.2	8.4	59.6
Serengeti *C. taurinus* average	21.0	17.7	38.7	nd	nd	61.4
Kobus ellipsiprymnus: Timbavati Reserve (1965) [l]	8.6	18.5	27.6	nd	nd	72.8
Kobus ellipsiprymnus: Timbavati Reserve (1966) [l]	28.6	34.6	63.2	nd	nd	36.8
Kobus ellipsiprymnus: Timbavati Reserve (1967) [l]	9.9	9.9	19.7	nd	nd	80.3
Timbavati *K. ellipsiprymnus* average	15.7	21.0	36.8	nd	nd	63.3

Abbreviation: nd = no data.

[a] Live count of males (3–1 yr = 116, 1–2 yr = 80, 2–3yr = 123, >3 yr = 300) from Spinage (1972:Table 3).

[b] Corrected number of males and females (0–1 yr = 2000, 1–2 yr = 1305, 2–3 yr = 1095, >3 yr = 4062) surviving to each age class from Spinage (1972:Table 4).

[c] Average of monthly live counts January-September 1960 from Dasmann and Mossman (1962:Table 4).

[d] Underwood (1975).

[e] Raw count of male and females skulls (0–1 yr = 5, 1–2 yr = 7, 2–3 yr = 7, 3–12 yr = 79, >12 yr = 32) from Spinage (1972:Table 5).

[f] 11 year average of population surveys (1974–1984) from Owen-Smith (2006:Fig. 1a).

[g] November 1964 (*n* = 652), April 1965 (*n* = 821), and April 1967 (*n* = 621) censuses from Hirst (1969:Table 16).

[h] 18 year (1978–1995) population survey average from Owen-Smith (2006:Fig. 1b).

[i] April 1965 (*n* = 3044), May 1966 (*n*=2660), and April 1967 (*n*= 2585) censuses from Hirst (1969:Table 7).

[j] Resident (*n* = 38342) and migratory (*n* = 65073) Serengeti counts from Ndibalema (2009:Table 1).

[k] Bunn and Gurtov (2014:Table 1) after Schaller (1972).

[l] April 1965 (*n* = 81), May 1966 (*n* = 269), and April 1967 censuses (*n* = 203) from Hirst (1969:Table 18).

Table 5

Fisher's exact and χ^2 tests comparing the frequencies of juvenile, prime adult, and old bovids killed by ambush and cursorial carnivores, and the pooled ambush and cursorial samples with the fossil assemblage samples. Significant probabilities are in bold. For all but the Kanjera vs. FLK-Zinj small bovid and the pooled ambush vs. FLK-Zinj large bovid comparisons the 95% CI of all samples with significant differences do not overlap in modified triangle plots (see Fig. 2 and SOM Fig. S1).

Ambush carnivores:

Small bovids killed by	Serengeti lion	Kafue lion	Serengeti leopard	Kafue leopard
Serengeti lion	—	0.8091	0.4793	0.6614
Kafue lion		—	0.3511	0.6122
Serengeti leopard			—	0.9436
Kafue leopard				—

Large bovids killed by	Serengeti lion	Kafue lion	Rwenzori lion	Kafue leopard
Serengeti lion	—	**0.0031**[a]	0.3386	0.8735
Kafue lion		—	0.6725	0.3445
Rwenzori lion			—	0.3439
Kafue leopard				—

Cursorial carnivores:

Small bovids killed by	Serengeti hyena	Serengeti cheetah	Serengeti wild dog	Kafue wild dog	Kafue cheetah
Serengeti hyena	—	**0.0008**	0.2143	**0.0092**	0.7018
Serengeti cheetah		—	0.2632	**0.0032**	0.1847
Serengeti wild dog			—	0.1022	0.8581
Kafue wild dog				—	0.3502
Kafue cheetah					—

Large bovids killed by	Serengeti hyena	Ngorogoro hyena	Serengeti wild dog	Kafue wild dog	Kafue cheetah
Serengeti hyena	—	**<0.0001**	**<0.0001**	0.6868	0.5973
Ngorogoro hyena		—	**<0.0001**	**0.0023**	0.1070
Serengeti wild dog			—	**<0.0001**	**<0.0001**
Kafue wild dog				—	0.6722
Kafue cheetah					—

Ambush vs. cursorial vs. Kanjera vs. FLK-Zinj vs. Olduvai background:

Small bovids	Ambush carnivores	Cursorial carnivores	Kanjera	FLK-Zinj	Olduvai background
Ambush carnivores	—	**<0.0001**[a]	0.5945[a]	**0.0012**	0.1225[a]
Cursorial carnivores		—	0.8311[a]	na[b]	**0.0010**[a]
Kanjera			—	**0.0156**	0.0912
FLK-Zinj				—	**0.0048**
Olduvai background					—
Large bovids					
Ambush carnivores	—	**<0.0001**[a]	**0.0314**[a]	**0.0457**[a]	0.3279[a]
Cursorial carnivores		—	**0.0044**[a]	na[b]	**0.0009**[a]
Kanjera			—	0.2242	0.3172
FLK-Zinj				—	0.6123
Olduvai background					—

[a] χ^2 was used because the total observed sample is > 300.

[b] χ^2 could not be performed due small sample size.

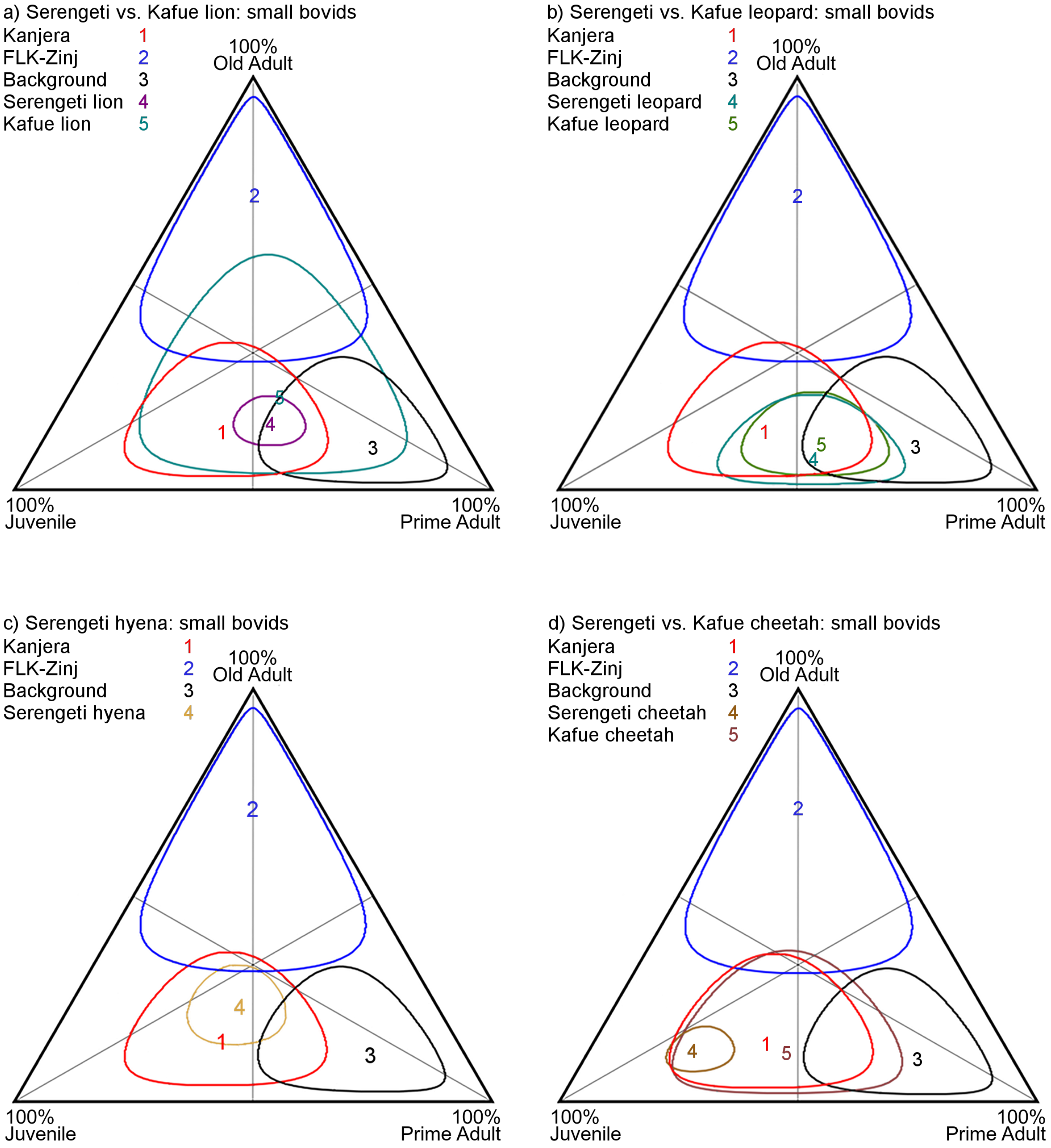
Supporting Online Material (SOM):

Bovid mortality patterns from Kanjera South, Homa Peninsula, Kenya and FLK-Zinj, Olduvai Gorge, Tanzania: Evidence for habitat mediated variability in Oldowan hominin hunting and scavenging behavior

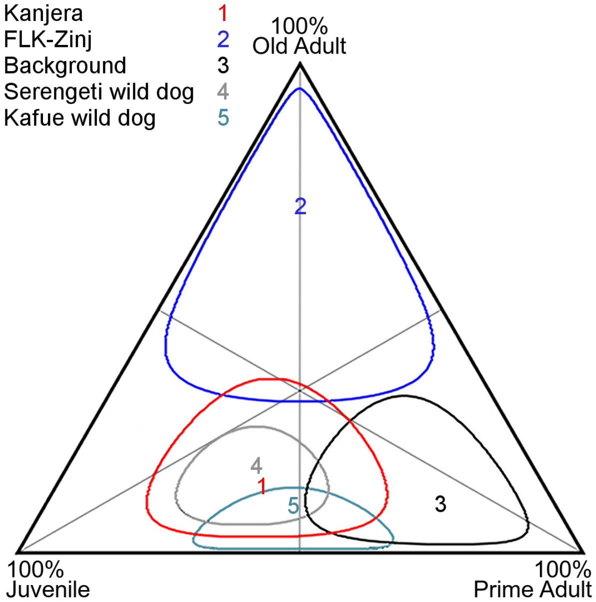
James S. Oliver [a,*], Thomas W. Plummer [b], Fritz Hertel [c], Laura C. Bishop [d]

[a] *Earth and Mineral Sciences Museum, Department of Geosciences, Pennsylvania State University, 207 Deike Building, University Park, PA 16802, USA*
[b] *Department of Anthropology, Queens College, CUNY and NYCEP, 65-30 Kissena Blvd, Flushing, NY 11367, USA*
[c] *Department of Biology, California State University, 18111 Nordhoff Street, Northridge, CA 91330, USA*
[d] *The Sino British College, University of Shanghai for Science and Technology, 1195 Middle Fuxing Road, Shanghai 20031, P.R. China* and *Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool, L3 3AF, UK*

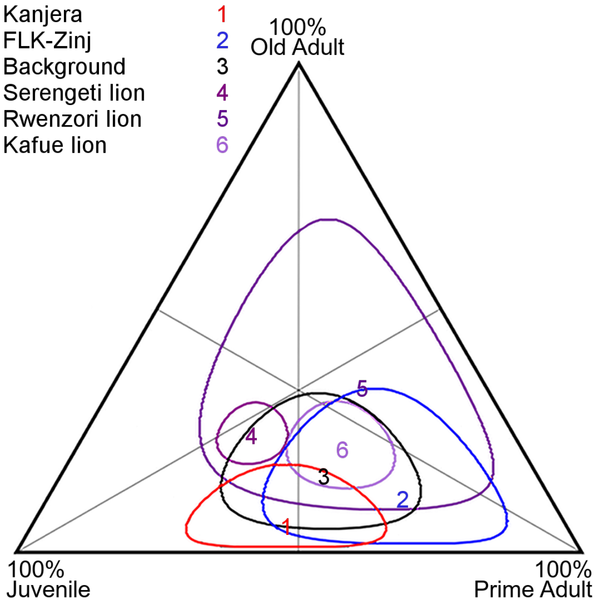
* Corresponding author.
E-mail address: joliver@museum.state.il.us (J.S. Oliver).


a) Serengeti vs. Kafue lion: small bovids
Kanjera 1
FLK-Zinj 2
Background 3
Serengeti lion 4
Kafue lion 5
100%
Old Adult
100%
Juvenile
100%
Prime Adult
b) Serengeti vs. Kafue leopard: small bovids
Kanjera 1
FLK-Zinj 2
Background 3
Serengeti leopard 4
Kafue leopard 5
100%
Old Adult
100%
Juvenile
100%
Prime Adult
c) Serengeti hyena: small bovids
Kanjera 1
FLK-Zinj 2
Background 3
Serengeti hyena 4
100%
Old Adult
100%
Juvenile
100%
Prime Adult
d) Serengeti vs. Kafue cheetah: small bovids
Kanjera 1
FLK-Zinj 2
Background 3
Serengeti cheetah 4
Kafue cheetah 5
100%
Old Adult
100%
Juvenile
100%
Prime Adult

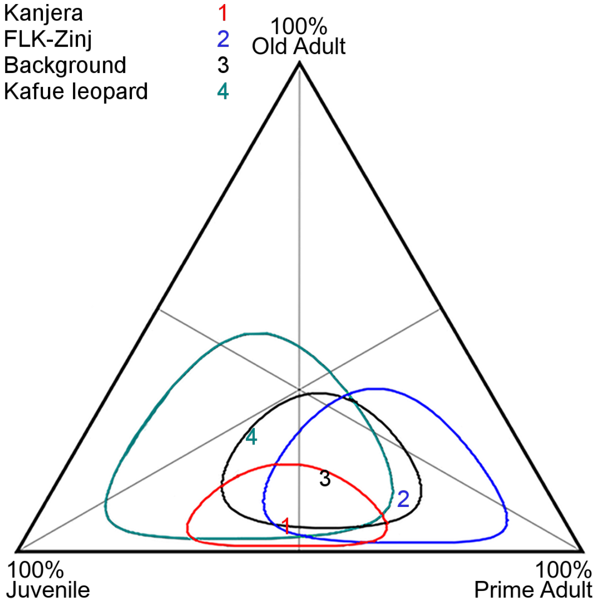
e) Serengeti vs. Kafue wild dog: small bovids



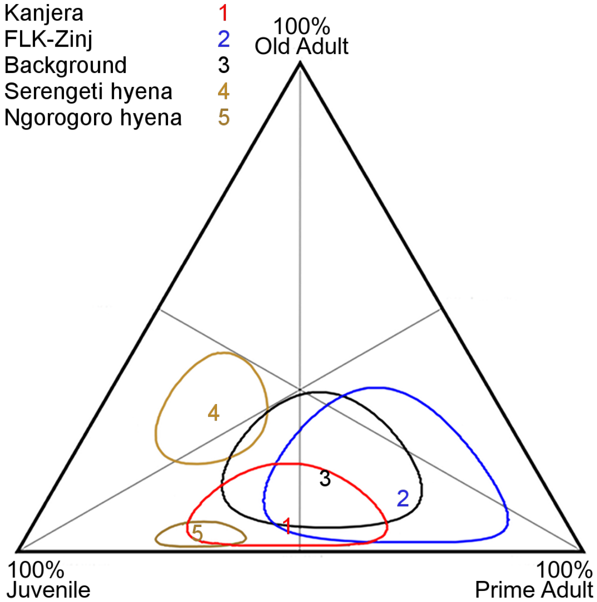
f) Serengeti vs. Kafue vs. Rwenzori lion: large bovids

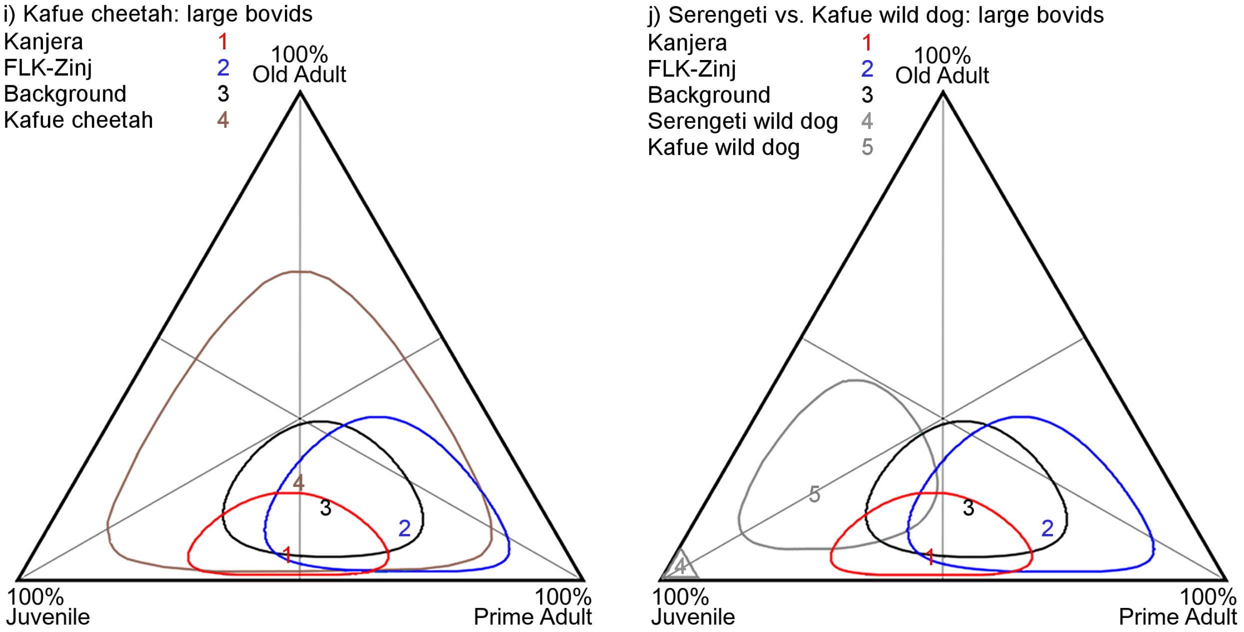


g) Kafue leopard: large bovids



h) Serengeti vs. Ngorogoro hyena: large bovids




i) Kafue cheetah: large bovids

j) Serengeti vs. Kafue wild dog: large bovids

SOM Figure S1. Modified triangle graphs showing variability in mortality patterns for small (a–e) and large (f–j) bovids killed by lions (a, f), hyenas (c, h), leopards (b, g), cheetahs (d, i), and wild dogs (e, j) in the Serengeti, Ngorogoro, Kafue, and Rwenzori (Table 3), compared to the Kanjera, FLK-Zinj, and the Olduvai Background assemblages (Table 2). Colored ellipses approximate the 95% confidence interval (CI) of each sample. The location of the numbered data point contained within an ellipse of the same color represents the percentage value of juvenile, prime-adult, and old individuals in each sample (the age proportions value).