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Zooarchaeology and Taphonomic Aspects of Later Stone Age Faunal Assemblage from Loiyangalani Site in Serengeti National Park, Tanzania

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Abstract

The paper presents detailed zooarchaeological and taphonomic results on the Later Stone Age (LSA) faunal assemblage. The contributions of various taphonomic agents in the formation of the assemblage are accentuated. The assemblage is well-preserved and the majority of specimens are not highly weathered. Fluvial disturbance did not play a significant role and can be ruled out as a significant taphonomic agent in the formation. Results indicate that LSA humans exploited high-quality nutritional resources mainly of the large-sized animals and aquatic resources as extra sources of meat and fat. The assemblage preserves stone tools butchery marks (cut marks and percussion marks) and carnivore marks (tooth marks) albeit few. Overall, the faunal assemblage exhibits high anthropogenic inputs and marginal carnivore involvement.

Keywords: Zooarchaeology, Taphonomy, Later Stone Age, Serengeti National Park, Loiyangalani, Tanzania.

Introduction

The Serengeti National Park is one of the homes to major archaeological cultural stages known in Eastern Africa (Figure 1). Research conducted within the park has reported cultural materials spanning the Early Stone Age (ESA), Middle Stone Age (MSA), Later Stone Age (LSA), Pastoral Neolithic (PN), Iron Age (IA), and rock paintings (Bower and Gogan-Porter 1981). Of note, Loiyangalani which is one of the few reported sites has received much of the archeological research attention (Bower 1977, Bower and Gogan-Porter 1981, Marean 1996, Bower et al. 1985, 2012, Thompson 2005, Bower and Mabulla 2013, Masele 2017, 2020, Maíllo-Fernández et al. 2019). Two major discrete archaeostratigraphic units have been identified at the site: the LSA (from 0 to 90 cm below the surface) at the top and the MSA (90 to 250 cm) below it (Masele 2017). No chronometric date for the LSA deposits exists, but in Eastern Africa can be as old as 40,000 BP (Ambrose 1998). Optically Stimulated Luminescence (OSL) dating has provided an age estimate of 65,000 BP for the MSA deposits (Feathers and Fusch 2005).

Studies of the Loiyangalani archaeological assemblages have recently made some noteworthy advances. Unfortunately, the emphasis has been mostly put on the studies of the MSA lithic assemblage typo-technological aspects (Bower et al. 2012, Bower and Mabulla 2013, Maíllo-Fernández et al. 2019) and its associated faunal assemblage (Marean 1996, Thompson 2005, Masele 2017, 2020). This paper provides detailed zooarchaeological and taphonomic results on the LSA faunal component recovered nearly two decades ago. The assemblage has been curated at the University of Dar es Salaam, Tanzania under the custody of Prof. Audax Z. P. Mabulla. It has remained unstudied and never fully reported.

Materials and Methods

A total of 21 test pits were established between 2003 and 2005 opening up about 19 m^2 of LSA deposits. Using 1 x 1 m squares with 5 mm spits excavations were mainly carried out. Sediments were dry-sieved through 5 mm meshes then handpicked for artefacts. A total of 333 fossilized faunal remains were unearthed. Mammal bones numerically dominated the sample. Other finds included fragmentary remains of fish, tortoises, crocodiles, rodents, and birds. This is rather a larger LSA faunal assemblage sample. Noticeably, Gifford-Gonzalez (1985) and Marean (1996) have previously studied only a total of 69 specimens from the LSA deposits.

Figure 1: Location of the Loiyangalani Site in the Serengeti National Park.

Zooarchaeological methods

Each specimen was identified to skeletal part level (e.g., humerus, tibia, etc). For identified skeletal parts: portion, symmetry, and state of epiphyseal fusion were recorded. Following Bunn (1982) guideline, specimens were assigned animal group sizes (sizes 1-4) and aggregated as small-sized (sizes 1-2) and large-sized (sizes 3-4) carcasses. As advocated by Domínguez-Rodrigo (1999), each animal size class was further split into five anatomical segments: cranial (including horn, skull, mandible, and teeth), axial (vertebra, rib, pelvis, and scapula), upper limb bones (humerus and femur), intermediate limb bones (radius and tibia), and lower limb bones (metacarpal and metatarsal).

The identified specimens are quantified as NISP, MNE, MNI, MAU, and %MAU (Binford 1981). To evaluate acquisition and carcass processing strategies by foragers, bivariate correlation between %MAU and

SFUI (Standardized Food Utility Index) values are performed (Metcalfe and Jones 1988). The high-survival elements, including the long bones and cranial elements are also considered because they survive better carnivore-ravaging and density-mediated attrition post-discard than most of the axial elements (Marean and Spencer 1991, Marean et al. 1992, Cleghorn and Marean 2004). Based on the proposal made by Faith and Gordon (2007), Shannon's evenness index was then calculated: $E = -\sum p_i * \ln p_i / \ln S$ where p_i represents the standardized proportion of specimens for the i-th element (MAU), S is the total number of elements present and E is the evenness index value. Subsequently, %MAU values are correlated with bone mineral density (BMD_2) values of an adult wildebeest (*Connachaetes taurinus*) to determine the degree of attrition the archaeological faunal assemblage underwent (Lam et al. 1999).

Taphonomic methods

Taking into account the nature of the site being located along a river course, it is logical to assume the faunal remains studied were potentially exposed to fluvial actions before finally buried. To determine the impacts of fluvial actions, skeletal part abundance (%MAU values) are correlated against Fluvial Transport Index (FTI) and Saturated Weight Index (SWI) (Behrensmeyer 1975, Frison and Todd 1986). The FTI and SWI values used are provided in Lyman (1994). Derived SWI whole bone values for reedbuck (*Redunca* sp.) and zebra (*Equus* sp.) are used as proxies for the small and large-sized animal subsamples, respectively.

Bone cortical surface preservation was subjectively scored as good, moderate, and poor. The study of bone weathering follows the standard scheme of Behrensmeyer (1978). Following Thompson (2005) protocol, post-depositional bone cortical surface degradation (sheen, smoothing, pocking, and exfoliation/sheeting) was also coded. The edges of each specimen were scored as fresh, slightly abraded, abraded, and very abraded. All specimens were also examined for discrete taphonomic signatures using hand lenses under a strong oblique light at a magnification of up to 15× (Blumenschine et al. 1996). Types were identified following the diagnostic criteria outlined by different scholars including stone cut marks (Binford 1981), hammerstone percussion marks (Blumenschine and Selvaggio 1988, Capaldo and Blumenschine 1994), tooth marks and rodent gnaw marks (Binford 1981, Blumenschine 1995), root-etching and biomechanical marks (Binford 1981, Domínguez-Rodrigo and Barba 2006), and trampling (Behrensmeyer et al. 1986). Only clear and unambiguous marks were recorded. Specimens with extensive concretion matrices coverage, root-marking, and exfoliated surfaces at a rate of > 75% of their total cortical surface areas are excluded in the tallies.

For the analysis of breakage patterns, only long bone fragments measuring ≥ 2 cm were considered. Each specimen was recorded as an estimate of the percentage of the remaining length (as < 25%, > 50%, > 75%, and 100%) and completeness of the shaft circumference (Type 1 preserves < 50%, Type 2 preserves > 75%, and Type 3 preserves 100%), to diagnose the agent of breakage and as an index of bone marrow extraction. The ratios of the sum of Type 2 and 3 shafts to the Type 1 shafts often range between 0.10 and 0.44 with the human generated faunal assemblages crowding at the lower end of the range (Bunn 1982).

Long bone fragments fracture margins were coded for breakage patterns following the typology criteria developed by Villa and Mahieu (1991) to determine the stage at which were fractured: fracture angles (as oblique, right, and intermediate), fracture outlines (curved, transverse, and intermediate), and fracture edges (smooth or jagged). Fracture angles and fracture outlines proportions are compared to calibrated experimental samples simulating hammerstone-only, hammerstone-to-carnivore, and carnivore-only foraging scenarios (Marean et al. 2000). They are also compared to archaeological faunal assemblages of known nature and degree of fragmentation of Sarrians and Fontbrégoua from southern France (Villa and Mahieu 1991). Sarrians is a late Neolithic site with a faunal assemblage fractured *in situ* (dry) via sediment compaction, and Fontbrégoua represents a faunal assemblage fractured by human while still fresh (green). To determine precisely the timeframe of breakage, Fracture Freshness Index (FFI) was also calculated following Outram (2002) protocol. An average FFI score of ≤ 2 is ascribed for a fresh (green) or human fractured faunal assemblage.

Results

Taphonomic profile of the faunal assemblage

The majority of specimens were fragmented. Only 9 were complete and mainly included carpals and tarsals. As shown in Figure 2, the assemblage exhibited a high proportion of specimens measuring < 3 cm and very few specimens measured > 4 cm. The mean length of the fragments was 1.4 cm. Faunal remains from archaeological sites located near or along rivers systems, as is a case for Loiyangalani are often characteristically biased towards a high proportion of large-sized specimens (Behrensmeyer 1975, Pante and Blumenschine 2010).

Identified skeletal parts fall between 1 and 3 cm in maximum length (NISP = 87, 79.82%). Specimens measuring < 1 cm accounted for 28.6% and 7.5% for the small-sized and large-sized animal subsamples, respectively (Figure 2). The small-sized animals subsample also exhibited a relatively high proportion of specimens in size class 1-2 cm but very few specimens measuring > 3 cm suggesting small-sized animal bones were intensively fragmented. There were relatively numerous specimens in size class 1-2 cm but progressively decrease in all the size classes measuring > 2 cm for the large-sized animals subsample. Of note, maximum length distribution appeared to vary between the small-sized and large-sized animal subsamples with the large-sized having relatively high proportions of specimens measuring > 3 cm (Figure 2). But, a Chi-square test shows the difference is statistically insignificant (χ^2 = 6.00, df = 4, p = 0.199).

Faunal remains are well-preserved (n = 184, 69.2% teeth excluded). Moderate and poor preserved accounted for 7.52% (n = 20) and 23.1% (n = 62), respectively of the total sample. As for identified skeletal parts, bone preservation was also excellent as about 76.84% (NISP = 73) had well-preserved cortical surfaces. The rest were moderately (9.47%, NISP = 9) or poorly preserved (13.68%, NISP = 13). A high soil pH of above 7 at the site created the favourable conditions for preservation. Identified skeletal parts exhibited a diverse array of bone weathering stages (2-4), epitomizing different deposition moments. The majority of specimens do not exceed stage 2 (NISP = 77, 81.05%), which suggests were buried quickly (Behrensmeyer 1978). Bones displaying advanced stage of weathering (stages 3-4) are quite few (NISP = 18, 18.95%). The common type of post-depositional bone cortical surface degradation recorded was exfoliation (NISP = 17, 73.9%) followed distantly by sheen (NISP = 6, 26.1%). Pocking and smoothing were relatively less common forms, with only 3 and 1 specimens, respectively displaying these marks. Faunal remains covered by calcareous matrix were less frequent (NISP = 7).

Strong negative correlation coefficients are recorded between %MAU and FTI values (Spearman's rho: small-sized, $r_s = -0.723$, p = 0.043, and large-sized carcasses, $r_s = -0.679$, p = 0.094), suggesting no significant fluvial disturbance of the archaeological faunal assemblage (Frison and Todd 1986). Nonetheless, a strong positive and statistically very significant correlation coefficient between %MAU and SWI values is registered for the small-sized animals subsample (Spearman's rho: $r_s = 0.896$, $p = < 0.010$). There is also a strong positive and nearly significant correlation coefficient for the large-sized animals subsample (Spearman's rho: $r_s = 0.771$, $p = 0.072$). The results denote water moved the bones of the small-sized and large-sized animals in their unsaturated (dry) state but not to a great distance (Behrensmeyer 1975). Specimens with signs of edge abrasion typical of the water-rolled were also less frequent (NISP = 36).

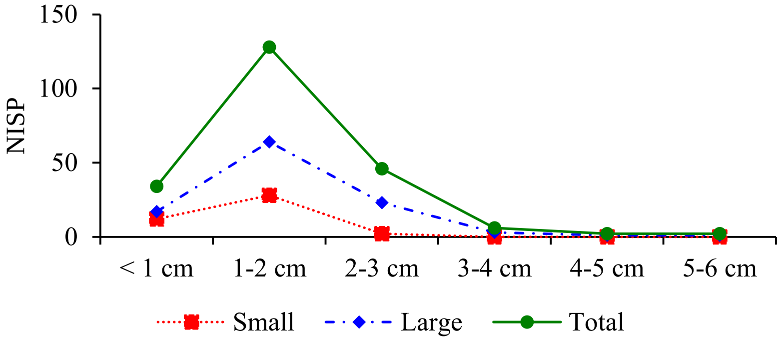

Figure 2: Size distribution of all specimens.

Skeletal part representation

A total of 194 mammalian specimens were identified to skeletal parts. Small-sized animals were generally represented by a relatively wide variety of elements than the large-sized animals (Table 1). All major five anatomical segments of a complete skeleton were represented, with the only exception being for size 4 animals (Table 2). As is the case for the numerous Stone Age sites in Eastern Africa, bovids dominate with at least 12 individuals represented. The representation was heavily weighted in favour of the large-sized animals (MNI = 9), which may denote their relative high importance in the human dietary spectrum (Table 3).

The axial and upper appendicular bones were the most frequent (NISP = 71). Lower limb bones and the cranial bones were scarcely represented (NISP = 38). Overall, rib fragments were the most identified (NISP = 38) followed distantly by isolated teeth, femur, metatarsal, and tibia fragments. Metacarpal, scapula, lumbar, radius, and sessamoid were rarely represented. The mandible, cervical, sacrum, cuneiform, navicular-cuboid, lunate, and second phalange were marginally represented with each being represented by a single specimen.

Long bone midshaft fragments were relatively more represented and their epiphyses were rare. The ratio of the epiphyses (n = 6) to the midshaft fragments (n = 35) excluding the complete bones was 0.17. The scarcity of epiphyseal portions may suggest the impacts of carnivore-ravaging and density-mediated attrition post-discard. Long bones abundance (%MAU values) correlated against corresponding %Survivorship values derived from a hyena-ravaged faunal sample (*sensu* Marean and Spencer 1991, Marean et al. 1992), yielded strong positive correlation coefficients for both animal size classes (Spearman's rho: small-sized, $r_s = 0.800$, $p = 0.200$, and large-sized carcasses, $r_s = 0.667$, $p = 0.219$). Spearman's rho also confirms the presence of a subsequent strong density-mediated attrition (small-sized, $r_s = 0.516$, $p = 0.295$, and large-sized carcasses, $r_s = 0.696$, $p = 0.125$). Plotting %MAU against density values involving all skeletal parts also yielded strong positive and very significant correlation coefficients (Spearman's rho: small-sized, $r_s = 0.545$, $p = 0.054$ and large-sized carcasses, $r_s = 0.779$, $p = < 0.010$). The results indicate the original skeletal part abundance had been significantly biased by both carnivore-ravaging and density-mediated attrition post-discard.

Plotting %MAU against SFUI values gave marginal positive but statistically insignificant correlation coefficients (Spearman’s rho: small-sized, r_s 0.462, $p = 0.152$, and large-sized carcasses, $r_s = 0.134$, $p = 0.731$), suggesting human selective transport of carcass parts with high nutritional values. When only high-survival elements are considered against their economic usefulness, relative strong positive correlations are recorded (Spearman’s rho: small-sized, $r_s = 0.971$, $p = < 0.010$, and large-sized carcasses, $r_s = 0.154$, $p = 0.804$). The coefficient of determination r^2 values of 0.943 and 0.024 for small-sized and large-sized carcass subsamples, respectively support the inference. The small-sized carcasses subsample yielded an evenness index of 0.92, which is an even distribution of the high-survival elements (MNE = 26). The value is consistent with an unbiased transport strategy of carcass parts that involved short-distance transport. The large-size carcasses subsample yielded an evenness index of 0.97, which also is an even distribution (MNE = 35). The value falls in the middle between the bulk and unconstrained transportation strategy of carcass parts in direct proportion to their economic utility that also involved short-distance transport (Faith and Gordon 2007).

Other taxa identified included fish, tortoises, and crocodiles and jointly make up 30% of the total NISP (Table 4). Of note, Catfish remains (*Clarias* sp.) often recovered from LSA deposits are the second most abundant taxon by 10% (Klein and Cruz-Uribe 1984, 1996). Tortoises accounted for about 7%. Isolated crocodile teeth represent the second common reptile taxon making up roughly 1%. A total of four isolated teeth represent remains of rodents. Rodents most likely entered the Loiyangalani faunal assemblage on their own, given the fact that they often live in burrows. Medium-sized bird remains (NISP = 6) along with the ostrich eggshell fragments (n = 23), were also recorded. It is not immediately clear whether the LSA humans at the site consumed the contents of the large ostrich eggs.

Table 1: Skeletal part representation

Element	Small-sized carcasses					Large-sized carcasses			
	Portion	NISP	MNE	MAU	%MAU	NISP	MNE	MAU	%MAU
Mandible		1	1	0.5	25	-	-	-	-
Tooth		1	-	-	-	13	-	-	-
Cervical V.		1	1	0.2	10	-	-	-	-
Lumbar V.		2	2	0.33	16.5	1	1	0.17	5.66
Sacrum V.		-	-	-	-	1	1	0.2	6.66
Rib		12	12	0.46	23	26	14	0.54	18
Scapula		2	1	0.5	25	2	1	0.5	16.7
Radius	*Midshaft*	1	1	0.5	25	-	-	-	-
	Distal	1	1	0.5	25	-	-	-	-
Metacarpal	*Midshaft*	1	-	-	-	4	4	2	66.66
Sesamoid		-	-	-	-	2	2	0.25	8.33
Femur	*Proximal*	1	-	-	-	1	1	0.5	16.7
	Midshaft	4	4	2	100	6	5	2.5	83.33
	Distal	1	1	0.5	25	-	-	-	-
Tibia	*Proximal*	1	-	-	-	1	1	0.5	16.7
	Midshaft	6	2	1	50	2	2	1	33.33
Metatarsal	*Midshaft*	5	3	1.5	75	6	6	3	100
Cuneiform		1	1	0.5	25	-	-	-	-
Nav. Cuboid		-	-	-	-	1	1	0.5	16.7
Lunate		-	-	-	-	1	1	0.5	16.7
Phalanx 2		1	1	0.13	6.5	-	-	-	-

Table 2: NISP by major anatomical sections and animal size

Section	Size 1	Size 2	Size 3	Size 4	Total
Cranial	1	1	13	-	15
Axial	7	9	21	9	46
Upper limb bone	3	3	6	1	13
Intermediate limb bone	7	2	3	-	12
Lower limb bone	1	8	4	10	23
Total	19	23	47	20	109

Table 3: NISP and MNI counts by animal size

Count	Size 1	Size 2	Size 3	Size 4	Total
NISP	19	23	47	20	109
MNI	3	4	5	4	12

Table 4: Other taxa identified

Taxa	Element	NISP
Fish	Neocranium	20
	Dentary	2
	Supracleithrum	1
	Vertebra	6
Rodent	Tooth	4
Tortoise	Carapace	20
Crocodile	Tooth	3
Bird	Coracoid	1
	Humerus	2
	Femur	3
	Ostrich eggshell	23

Human bone surface modifications

Butchery marks were noted on a very few specimens but more prevalent on the large-sized animals. They include cut marks and percussion marks (*n* = 11) and collectively establish human involvement with the bones while still in their nutritive state. A total of 7 specimens preserved cut marks. Overall, cut marks affected 3.9% of the total mammalian NISP (teeth and rodents excluded).

The locations and forms of cut marks permit identification of some butchering activities (Binford 1981, Nilssen 2000). The cut marks preserved on ribs correspond to filleting operations. Cut marks on metapodials suggest were made during skinning of the carcasses. Of note, the majority of cut marks on limb bones occur on midshaft sections (*n* = 5) where are interpreted as evidence for filleting/deboning activities (Domínguez-Rodrigo 1999, Galán and Domínguez-Rodrigo 2013). Of note, the midshafts of the metacarpal and metatarsal, which typically yield little meat, preserve high incidences of cut marks (*n* = 4). Cut marks on these elements mostly correspond to preparation for hammerstone fracturing to extract bone marrow (Bunn 1982). Nonetheless, a femur of a large-sized animal exhibited slicing marks on its midshaft, which suggests LSA humans enjoyed regular access to the meatier parts of the carcasses. This observation may also hint they processed nearly complete or complete carcasses (Domínguez-Rodrigo 1999, Domínguez-Rodrigo and Barba 2007).

Bone marrow harvesting is a well-known foraging activity for Stone Age hunter-gatherers (Binford 1981, Bunn 1982, Blumenschine 1995) and Loiyangalani site is no exception of this. Virtually all marrow-rich long bones are fractured. Percussion notches (*n* = 4) were recorded on metatarsals of the large-sized animals preferentially on their midshaft sections suggesting LSA humans regularly extracted bone marrow (Blumenschine 1995, Galán et al. 2009). A single metatarsal belonging to the small-sized animal also exhibited a percussion notch (Table 5).

Of the total 40 long bone fragments analyzed, a total of 35 were Type 1 shafts. The remaining were Type 2 and Type 3 shafts. The ratio of the sum of Type 2 and 3 shafts to the Type 1 shafts is 0.14, which falls at the lowermost end of the range denoting anthropogenic agency of breakage (Bunn 1982). The majority of the fractures on long bone shaft fragments exhibited green fractures (73%), which denotes were fractured while still fresh (green) to extract the within-bone nutrients. Diagenetic fractures, which mostly affect mineralized (dry) bones occur in low proportion (27%) and can be mostly attributed to the impacts of sediment compaction and animal trampling by migrating ungulates. As seen in Figures 3 and 4, the oblique angles and V-shaped outlines proportions are well above the Sarrians archaeological faunal assemblage post-depositionally fractured (dry) via sediment compaction (Villa and Mahieu 1991). Besides, the majority of specimens had total FFI scores of ≤ 2 with a cumulative proportion of roughly 71%, which implies were fractured while still in relatively fresh (green) state certainly during bone marrow extraction (Table 6). Splitting the FFI score into small-sized and large-sized animal subsamples, the respective cumulative proportions are 57.14% and 84.21%. Very few specimens (*n* = 4) displayed mixed fractures (green and dry), which also suggests some were fractured while gradually becoming dry (Table 6). Specimens with unfresh fractures accounted for 20%. An average FFI score for the assemblage is 1.58, which falls within the range of anthropogenic fractured faunal assemblage (see Table 6 for the details).

Table 5: Human and carnivore bone surface modifications

Element	Cut marks		Percussion marks		Tooth marks	
	Small	Large	Small	Large	Small	Large
Rib	1	1	-	-	-	1
Metacarpal midshaft	-	2	-	-	1	-
Femur midshaft	-	1	-	-	-	-
Metatarsal midshaft		2	1	3	1	1
Total	1	6	1	3	2	2

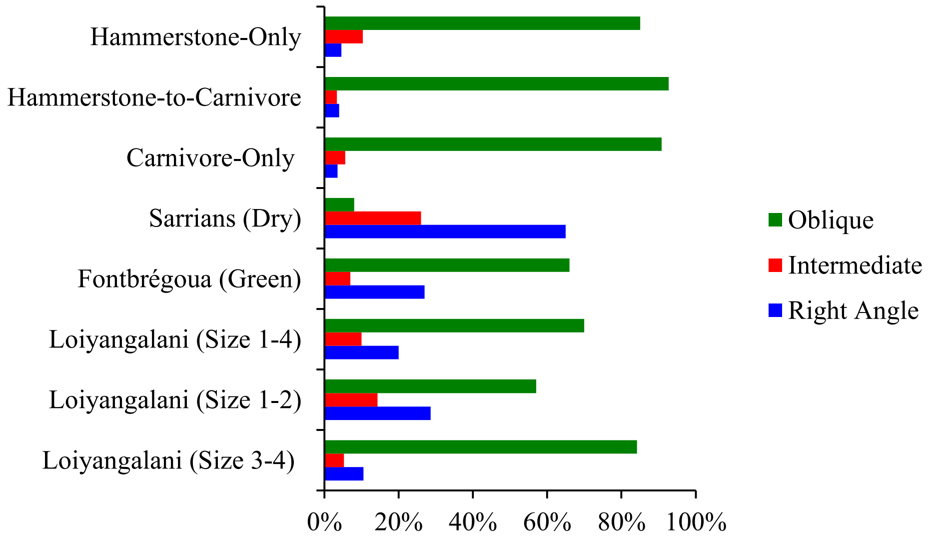

Figure 3: Long bone fracture angles compared to several experimental and archaeological samples.

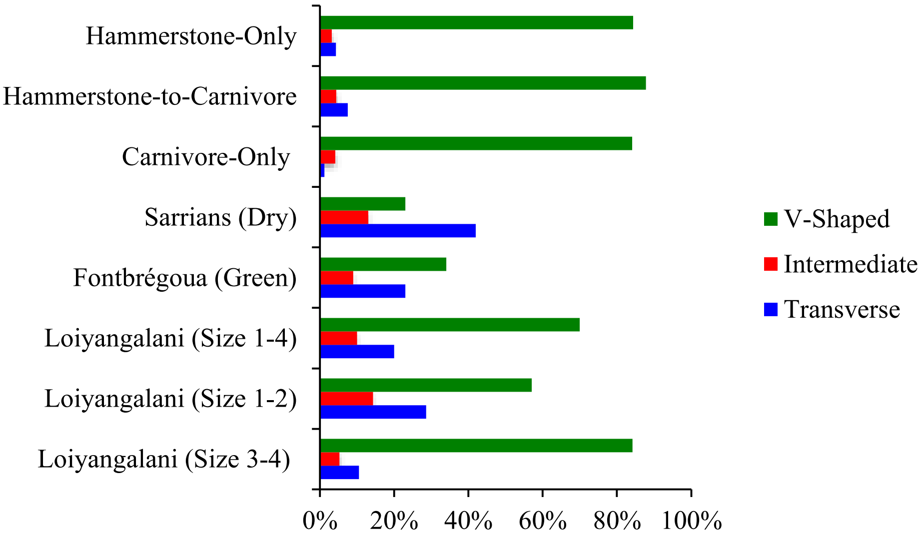

Figure 4: Long bone fracture outlines compared to several experimental and archaeological samples.

Table 6: FFI scores cumulative frequencies and averages by animal size

FFI Score	Small		Large		Total	
	NISP	%NISP	NISP	%NISP	NISP	%NISP
0	12	57.14	16	84.21	28	70.00
1	-	-	-	-	-	-
2	-	-	-	-	-	-
3	1	4.76	-	-	1	2.50
4	2	9.53	1	5.26	3	7.50
5	-	-	-	-	-	-
6	6	28.57	2	10.53	8	20.00
Total	21	100	19	100.00	40	100.00
Average FFI Score	2.24		0.84		1.58	

Non-human bone surface modifications

Carnivore tooth marks were markedly very few. Only a total of 4 specimens preserved definite tooth marks. Tooth scores and pits were the most common types identified. Metacarpal and metatarsal midshaft fragments have relatively high incidences of tooth marks (n = 3). A rib fragment also preserved a tooth mark score. Spotted hyenas (*Crocuta crocuta*) are responsible for the damage as attested by the dimensions of the inflicted tooth markings (*sensu* Domínguez-Rodrigo et al. 2012). Overall, carnivore damage affected 4.2% of total mammalian NISP (teeth and rodents excluded). Faunal remains exclusively processed by carnivores generate high proportions of tooth marks often exceeding 35% on small-sized and 50% on medium-to-large-sized carcasses (Blumenschine and Marean 1993, Capaldo 1997).

Traces of other taphonomic agents are summarized in Table 7. The activities of rodents appear to be limited as only single specimen exhibited diagnostics gnaw marks. Trampling marks (n = 5) were also recorded. Root marks are more common on unidentified specimens. They also affected a total of eight identified skeletal parts and were mostly noted on bone cortical surfaces and in the marrow cavities. This suggests the presence of a densely vegetated ground cover at the site during the deposition of the faunal remains. A single indeterminate specimen also exhibited biochemical marks typically resulting from fungi and bacteria colonies (*sensu* Domínguez-Rodrigo and Barba 2006). No instance of carnivore digestion was registered on any bone in the assemblage.

Table 7: Other non-human surface modifications

Element	Rodent marks	Root marks	Biochemical marks	Trample marks
Rib	-	5	-	2
Scapula	-	-	-	2
Metacarpal	-	1	-	-
Tibia	1	2	-	-
Unidentifiable	-	10	1	1
Total	1	18	1	5

Discussion

The archaeological faunal assemblage studied is highly fragmented which is an eminent feature of human generated accumulations (Binford 1981, Bunn 1982, Blumenschine 1995). The assemblage also underwent significant post-discard carnivore interventions and density-mediated attrition. The prevalence of specimens measuring < 4 cm suggests low-energy fluvial deposition context of the faunal assemblage and an absence of hydrodynamic sorting (Behrensmeyer 1975, Pante and Blumenschine 2010).

Skeletal part representation shows Later Stone Age humans selectively transported and exploited high-meat and marrow-yielding carcass parts of the small-sized and large-sized ungulates. The axial and upper appendicular limb bones dominate the identified skeletal parts. Skeletal part abundance involving all elements and the high-survival elements are positively correlated with their economic utility. This pattern is more consistent with a foraging strategy, which is more oriented towards maximization of the foraging returns (Kelly 2007). The fact that, only a proximal radius belonging to a size 2 bovid was recorded unfused does not merit drawing robust conclusion on the mortality profile of the ungulates hunted by the LSA people. The observed pattern can be ascribed to the impacts introduced by carnivore-ravaging, density-mediated attrition, and can also mirror the extent and intensity of fragmentation of the faunal assemblage (Klein and Cruz-Uribe 1984).

Overall traces of human and carnivore modifications are scarce and only accounted for < 5% on identified skeletal parts. The sample size of cut-marked and tooth-marked skeletal parts is also extremely too small to evaluate their distribution across complete skeletons of the small-sized and large-sized animals (Table 5). Long limb bone fragments bearing butchery (cut marks and percussion marks) and carnivore marks (tooth marks) on their midshaft sections are also very few (*n* = 12) and preclude the discrimination of the order of access (early/primary or late/secondary) to the carcasses by humans and carnivores (Blumenschine 1995, Marean et al. 2000, Pante et al. 2012). Nonetheless, they bear relatively high incidences of butchery (*n* = 9) compared to carnivore marks (*n* = 3). The results are astonishing given the open nature of the Loiyangalani site and its location along the wildlife migration. Hyenas and lions should have initially processed the bones deposited at the site. The Serengeti National Park has approximately 3,000 lions and 10,000 hyenas roaming the Serengeti plains (Caro and Durant 1995). The low proportion of tooth marks in the assemblage can be attributed to different factors, including carnivore-feeding behaviour.

According to Kruuk (1972), spotted hyenas habitually hoard meat or bones in still muddy water so that other predators and scavengers cannot steal them. As a result, they may get lost. The low proportion may also reflect the high degree of fragmentation of the faunal assemblage. Besides, crocodiles also identified in the faunal assemblage frequently consume whole or leave the whole bones behind that may or may not have tooth marks while feeding (Njau and Blumenschine 2006). They also rarely break ungulate bones while feeding. Rodent gnaw marks are also rare and are present on < 1% of the total NISP suggesting their involvement was minimal.

Conclusion

The faunal assemblage studied offer additional insights on Later Stone Age humans foraging economy within the Serengeti National Park. Judging from the skeletal representations, fragmentation patterns, and the dearth of carnivore marks compared to butchery marks all point towards an anthropogenic origin of the faunal assemblage. It is argued elsewhere that LSA people effectively exploited aquatic resources, which also appears to be the case at Loiyangalani (Klein and Cruz-Uribe 1984, 1996). Tortoise and fish remains identified in the faunal assemblage are most likely the results of human foraging activities perhaps as extra sources of meat and fat.

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