



ELSEVIER

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

A taphonomic analysis of PTK (Bed I, Olduvai Gorge) and its bearing on the interpretation of the dietary and eco-spatial behaviors of early humans

Elia Organista ^{a, b, *}, Abel Moclán ^{b, c, d}, Julia Aramendi ^{b, e}, Lucía Cobo-Sánchez ^{b, f}, Charles P. Egeland ^g, David Uribebarrea ^{b, h}, David Martín-Perea ^{b, i}, Marina Vegara-Riquelme ^{b, j}, Lucía Hernández-Vivanco ^b, Agness Gidna ^k, Audax Mabula ^l, Enrique Baquedano ^{b, m}, Manuel Domínguez-Rodrigo ^{b, n, o}

^a Osteoarchaeological Research Laboratory, Department of Archaeology and Classical Studies, Stockholm University, 106 91, Wallenberglaboratoriet, Stockholm, Sweden

^b Institute of Evolution in Africa (IDEA), University of Alcalá de Henares, Covarrubias 36, 28010, Madrid, Spain

^c Centro Nacional de Investigación Sobre La Evolución Humana (CENIEH), Paseo Sierra de Atapuerca 3, 09002, Burgos, Spain

^d Escuela Interuniversitaria de Posgrado en Evolución Humana, Universidad de Burgos, Don Juan de Austria 1, 09001, Burgos, Spain

^e Department of Cartographic and Land Engineering, Universidad de Salamanca, 05003, Ávila, Spain

^f Computational Archaeology (CoDArchLab) Institute of Archaeology, University of Cologne, Albertus-Magnus-Platz D-50923, Cologne, Germany

^g Department of Anthropology, University of North Carolina at Greensboro, Greensboro, NC, USA

^h Geodynamics, Stratigraphy and Palaeontology Department, Complutense University of Madrid, José Antonio Novais 12, 28040, Madrid, Spain

ⁱ Paleobiology Department, National Natural Sciences Museum—CSIC, José Gutiérrez Abascal 2, 28006, Madrid, Spain

^j University of Alcalá, Department of History and Philosophy, Prehistory Area, C/Colegios 2, 28801, Alcalá de Henares, Spain

^k Paleontology Unit, National Museum of Tanzania in Dar Es Salaam, Robert Shaban St, P.O. Box 511, Dar Es Salaam, Tanzania

^l Department of Archaeology and Heritage Studies, University of Dar Es Salaam, P.O. Box 35050, Dar Es Salaam, Tanzania

^m Regional Archaeological Museum of Madrid, Plaza de Las Bernardas S/n, Alcalá de Henares, Spain

ⁿ Department of Anthropology, Rice University, 6100 Main St., Houston, TX, 77005-1827, USA

^o Area of Prehistory (Department History and Philosophy), University of Alcalá, 28801, Alcalá de Henares, Spain

ARTICLE INFO

Article history:

Received 19 April 2022

Received in revised form

8 November 2022

Accepted 4 December 2022

Available online 15 December 2022

Handling Editor: Danielle Schreve

Keywords:

Taphonomy

Olduvai gorge

Early pleistocene

Meat-eating

ABSTRACT

Here, we present a thorough taphonomic analysis of the 1.84 million-year-old site of Phillip Tobias Korongo (PTK), Bed I, Olduvai Gorge. PTK is one of the new archaeological sites documented on the FLK Zinj paleolandscape, in which FLK 22 level was deposited and covered by Tuff IC. Therefore, PTK is penecontemporary with these sites: FLK Zinj, DS, AMK and AGS. The occurrence of these sites within a thin clay unit of ~20 cm, occupying not only the same vertically discrete stratigraphic unit, but also the same paleosurface, with an exceptional preservation of the archaeological record in its primary depositional locus, constitutes a unique opportunity to explore early hominin behavioral diversity at the most limited geochronological scale possible. The Olduvai Bed I sites have been the core of behavioral modelling for the past half a century, and the newly discovered sites, excavated with 21st century technology, will increase significantly our understanding of early human adaptive patterns. Here, we present PTK as another assemblage where faunal resources were acquired by hominins prior to any carnivore, and where stone-tool assisted bulk defleshing was carried out. The abundance of juvenile individuals extends our understanding, as in Kanjera (Kenya), about the hunting skills of early *Homo sensu lato*. The increasing number of sites, where bulk defleshing of small and medium-sized carcasses took place is underscoring the importance of meat in the diets of some of the early hominins, and their patterned use of the space for food processing and consumption. The patterning emerging has a profound importance

* Corresponding author. Osteoarchaeological Research Laboratory, Department of Archaeology and Classical Studies, Stockholm University, 106 91, Wallenberglaboratoriet, Stockholm, Sweden.

E-mail address: elia.organista.labrado@ofl.su.se (E. Organista).

for the evolution of some of the features that have traditionally been used to identify the behavior of the genus *Homo*.

© 2022 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Hominin primary or secondary access to carcasses has important implications for the reconstruction of the behavior of early *Homo sensu lato*. Early access to carcasses would imply regular meat-eating, and it might have promoted food-sharing and other cooperative behaviors (Isaac, 1978, 1983). In contrast, secondary access to largely defleshed carcasses would have provided limited surplus resources (Speth, 1989; Blumenschine and Madrigal, 1993; Domínguez-Rodrigo, 1999; Domínguez-Rodrigo et al., 2014a; Gidna et al., 2014), which, in turn, would have prevented food-sharing and, probably, the development of further complex cooperative behaviors. For decades, FLK Zinj (Bed I, Olduvai Gorge) has been used as the main testing background to infer features of early *Homo* behavior. Ethnographic analogues and experimental studies applied to the analysis of this site have led to different interpretations about primary versus secondary access of hominins to carcasses (e.g., Binford, 1985; Bunn, 1986; Bunn and Kroll, 1986; Blumenschine, 1986; Domínguez-Rodrigo, 1997a; Capaldo, 1998a; Pante et al., 2012; Parkinson, 2018).

Through the use of skeletal part profiles, some researchers have argued that hominins had early access to carcasses, and that they selectively were transporting high-yielding carcass parts (Isaac, 1978, 1983; Bunn, 1981, 1982, 1983, 1991; Bunn and Kroll, 1986, 1988; Potts, 1988; Bunn and Ezzo, 1993; Oliver, 1994; Rose and Marshall, 1996; Domínguez-Rodrigo, 1997a; Domínguez-Rodrigo and Pickering, 2003; Bunn and Pickering, 2010). Using the same skeletal profiles, other researchers have argued that hominins had secondary access to partially or fully defleshed carcasses (Capaldo, 1995, 1997), that hominins scavenged carcasses initially accumulated by other carnivores at kill-sites or dens (Binford, 1981), or that hominins scavenged the brain and marrow-bearing bones from defleshed felid kills and transported them to refuges (Blumenschine, 1986, 1991, 1995; Blumenschine et al., 1994; Selvaggio, 1994). In order to overcome the equifinality produced by skeletal part profiles, some researchers focused on the analysis of bone surface modifications and bone breakage patterns. Blumenschine (1988, 1995) experimentally argued that the frequencies of tooth-marked specimens by limb bone portion could be an indicator of the order of carnivore access to carcass resources. However, more recent research has shown that tooth mark frequencies can be similar in carnivore-to-hominin and hominin-to-carnivore experimental models when felids rather than hyenas are the primary agent in carcass modification (Domínguez-Rodrigo et al., 2007a; Organista et al., 2016). Additionally, cut-marked bones have been interpreted as the result of hominins exploiting whole fleshed carcasses (Bunn and Kroll, 1986), or the outcome of removing marginal scraps of flesh that survive after carnivore consumption (Blumenschine, 1991, 1995). This purported equifinality is methodological and can be overcome by quantifying the frequency and anatomical distribution of cut marks per bone section and element combined (Domínguez-Rodrigo, 1997b; Domínguez-Rodrigo et al., 2007b). Recent Machine Learning (ML) techniques have also been effectively used to solve some of these taphonomic challenges (e.g., Cifuentes-Alcobendas and Domínguez-Rodrigo, 2019; Domínguez-Rodrigo et al., 2020). Recently, we carried out a 3D and deep learning analysis of cut

marks on limb bones to the upper level (equivalent to FLK Zinj's level 22A) of FLK Zinj, PTK and level 22B of David's Site (DS), and the results indicate that hominins might have had primary access to carcasses (Domínguez-Rodrigo et al., 2021). However, in this previous work different important aspects, like carcass acquisition strategies or what type of carnivores intervened in the PTK site were not tested. That study was also limited to the analysis of cut marks and excluded all the other taphonomic variables that inform us about site formation processes.

David's Site (DS) is a new site located on the same paleolandscape as FLK Zinj. Recent taphonomic analyses of the DS faunal assemblage indicate that hominins had early access to carcasses (Cobo-Sánchez, 2020; Domínguez-Rodrigo et al., 2021). They transported complete or partial carcasses to the site to be processed and potentially consumed collectively (Cobo-Sánchez, 2020). PTK, also contemporaneous with DS, shows the same spatial properties (i.e., mono-cluster) as FLK Zinj (Domínguez-Rodrigo and Cobo-Sánchez, 2017a). The site presents an exceptional preservation of the archaeological materials and bone cortical surfaces, which offers the possibility of testing previous interpretations about carcass acquisition strategies, and shedding new light on early *Homo* behavior. It can also contribute to widening the range of behaviors documented at these early sites. The main aim of the present work is to provide new evidence to understand carcass acquisition strategies by early humans and the potential impact of meat consumption in their diets. Additional questions that will be addressed in the present study are: What function did early Oldowan sites have in the socio-economic structure of early humans? Is there any patterning in how early humans used the space in these *loci* and in the activities that they carried out in them or do they display wide variability? How can we use these early sites to understand better the lifestyle and behaviors of early *Homo sensu lato*?

2. The PTK site and its archaeofaunal assemblage

PTK is located on the north side of the secondary gorge, just upstream from the junction with the main gorge of Olduvai Gorge, Tanzania (Fig. 1). The site is situated 370 m south of the FLK Zinj and 330 m westward of DS (Domínguez-Rodrigo et al., 2017). Its chronology is well constricted by two volcanic tuffs: tuff IB and tuff IC, which have been dated by argon-argon ($^{40}\text{Ar}/^{39}\text{Ar}$) to 1.848 ± 0.003 Ma and 1.848 ± 0.008 Ma respectively (Deino, 2012). In the present study, we focus on the archaeological material that is within the same clay stratum and same paleosurface as FLK Zinj (upper Zinj or level 22A). The Zinj clay consists of a minimum of two clay depositional events, each containing separate archaeological levels formed at different times with mainly similar environmental conditions. Level 22A shows a more hydrologically closed system than level 22B, but both levels were deposited under a very low-energy conditions (Martín-Perea et al., 2019). Each archaeological level is distributed over a maximum vertical depth of 10 cm (most commonly less). The apparent vertical distribution of materials shown in Fig. 1 is due to the tilting of the modern terrain caused by tectonics occurring after site formation. Paleogeographically, PTK had a slightly elevated profile, compared to the adjacent lake margin, and the area was probably well-drained during the wet season, showing runoff shapes, like rills and small

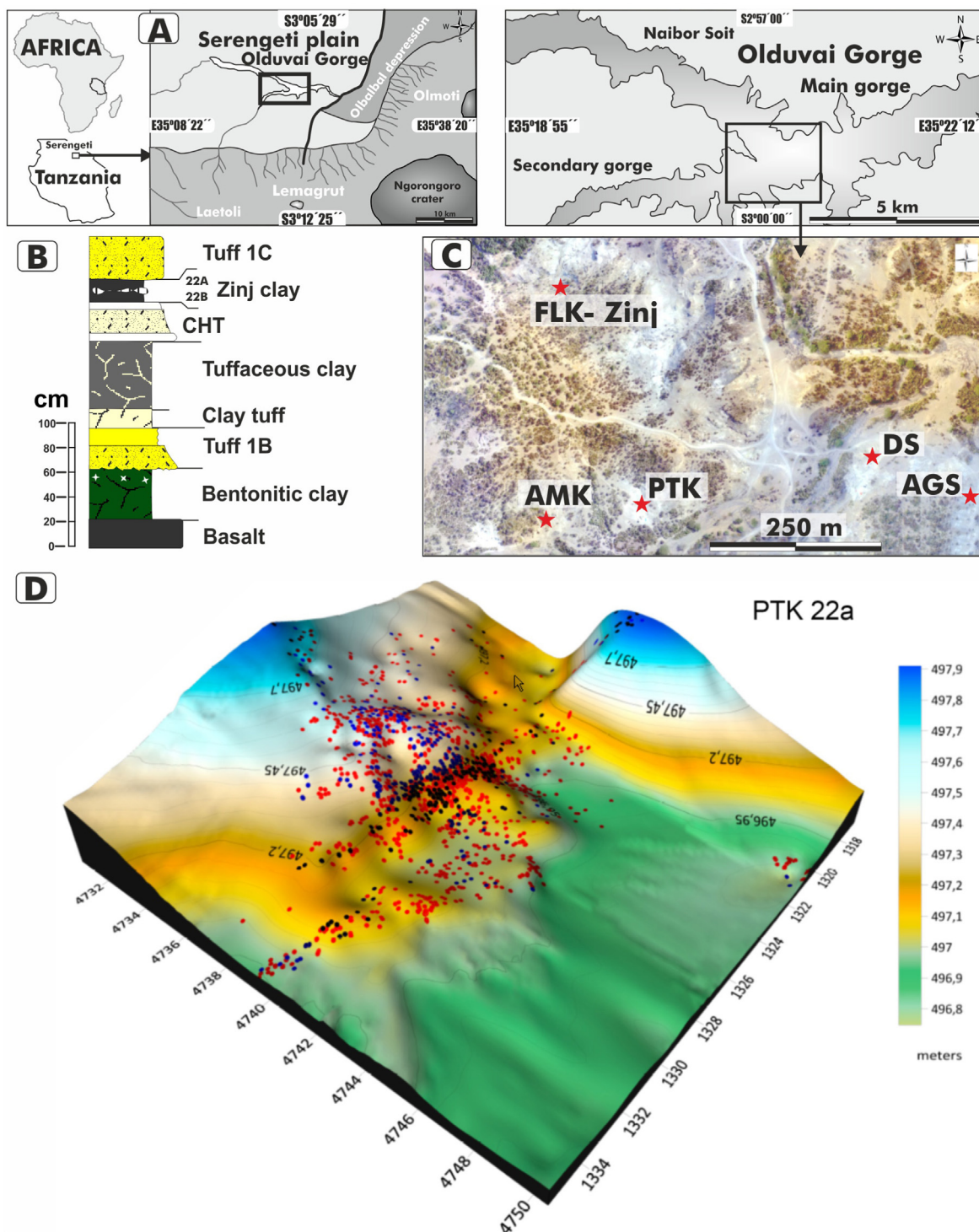


Fig. 1. A) Location of PTK in the Olduvai Gorge. B) Detailed stratigraphic section of PTK with the archaeological levels 22A and 22B. C) Topographic model of PTK with the distribution of bone (red points) and lithic (blue point) remains at level 22A. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

depressions (Uribelarrea et al., 2014) that resulted in alkaline soil conditions which optimised bone-surface preservation (Pizarro-Monzo et al., 2021).

From 2012 to 2019, an open excavation consisting of twenty-six adjacent trenches was carried out at PTK unearthing an area of 185 m² (Fig. 2). Small hand tools were utilized for the excavation of the fossiliferous levels and all the sediments were systematically

sieved using 5 mm and 3 mm screen-meshes. Stone tools and fossil bones ≥ 2 cm and identifiable remains < 2 cm, were plotted with a laser total station. The humidity of the sediments had affected some of the fossil bones, which presented cracks and recent breakage planes that ultimately resulted in the fragmentation of some specimens as they were removed from the soil. However, when possible, bone specimens risking fracture during excavation were

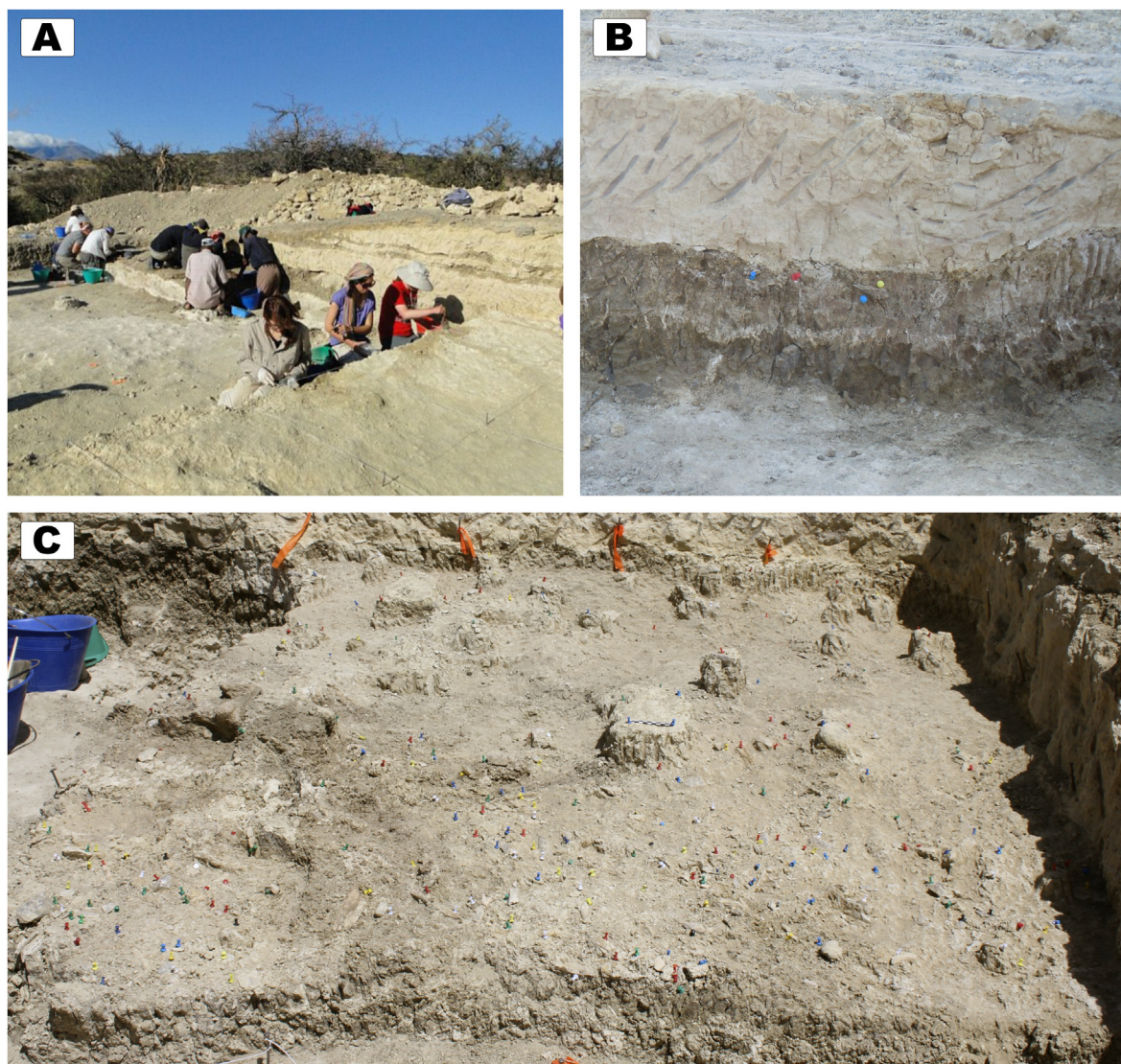


Fig. 2. PTK site with a detailed of its stratigraphy and the archaeological materials discovered in trench 10 level 22A.

consolidated with Paraloid B72® (5–10% dissolved in acetone). Additionally, to preserve the morphological structure of some fossil remains, it was necessary to apply gauze before their removal. Some specimens show chemical weathering because they were diagenetically exposed to a constant variation of humidity within the soil matrix. These were mainly found in the northeast area of the archaeological site, where Tuff 1C had been affected by erosion.

In this work, we present the results of the analyses on the faunal materials recovered in level 22A (PTK's upper level). This level is composed of a dense accumulation of fossil bones ($n = 1514$) and stone artefacts. Flakes and flake fragments represent the bulk of the lithic assemblage ($n = 497$) (Fig. 3).

3. Methods

3.1. Age profiles

To establish dental age of faunal remains, two methods were used considering the different taxa and following the approach detailed by Spinage (1967, 1976) for waterbuck and gazelle; Talbot and Talbot (1963) and Attwell (1980) for wildebeest; Grobler (1980)

for Hipotragini remains; and Loch and Bradley (1998) and Marín et al. (2017) for equids. First, the degree of the eruption of deciduous teeth and the eruption and development of permanent teeth was explored. Second, the degree of tooth wear was estimated. Both processes were explored under the assumption that tooth eruption and wear are similar in the mandible and the maxilla, though it is known that they are slightly different (Spinage, 1967, 1976). Thus, it is possible that the individuals catalogued using mandibles are slightly older than reported here. However, this bias has not affected the determination of age groups in the present study. Table S1 shows the potential ecological lifespan in years for the different species considered in this analysis and Table S2 shows the material that was used to determine the minimum number of individuals (MNI). We examined 35 isolated dental pieces and 33 teeth anchored in their mandibular or maxillary alveoli to determine the mortality profiles of the bovids ($n = 64$) and one equid ($n = 4$) recovered from level 22A.

The age profiles were analyzed by means of several methods, including ternary diagrams (Stiner, 1990), Principal Component Analysis (PCA), and Canonical Variate Analysis (CVA), which were used to compare PTK mortality profiles with age profiles derived

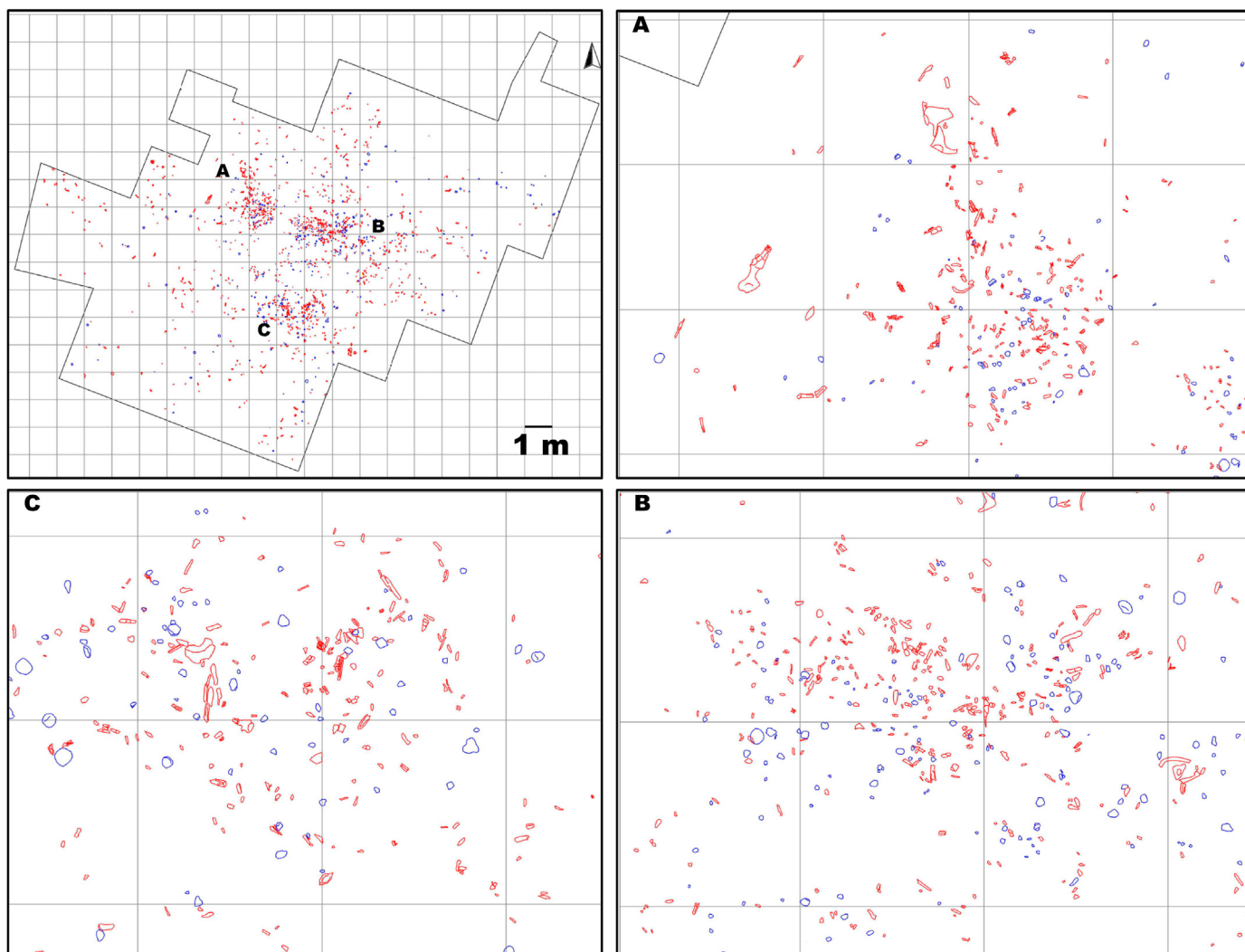


Fig. 3. Spatial distribution of the archaeological materials in level 22A (red = bones; blue = lithics). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

from studies with carnivores -lion, hyena, leopard, wild dog- (Bunn and Pickering, 2010), modern foraging ethnographic samples -Hadza and Kua- (Bunn and Gurtov, 2014), and archaeological assemblages -FLK Zinj, DS and Kanjera- (Cobo-Sánchez, 2020; Oliver et al., 2019).

Individuals were also assigned to five age groups based on their potential ecological longevity (PEL) (Bunn and Pickering, 2010), but given that the MNI obtained from teeth differs from postcranial MNI, we sorted the age groups into three: juvenile, prime adult and old adult. The different corners of the triangular diagram represent 100% of each age category. Between these corners, two zones indicate the attritional (left side) and catastrophic (right side) profiles (although see Discamps and Costamagno, 2015, because their mathematical simulations identified potential problems in the zoning of ternary diagrams). The attritional profile is represented by very young and old individuals, while prime adults are relatively rare. This pattern has been associated with cursorial predators such as cheetahs, wild dogs and hyaenas (Stiner, 1990). The catastrophic or living profile is represented mainly by prime-adult individuals with progressively fewer individuals belonging to other age classes, emulating the structure of a living population (Klein, 1982). This pattern is associated by Stiner (1990) with ambush predators. The

software uses maximum likelihood statistics to produce a density contour that is sensitive to sample size and approximated to the 95% confidence interval (Steele and Weaver, 2002).

The second method is a combination of Principal Component Analyses (PCA) and Canonical Variate Analyses (CVA), which reduce the dimensionality of the original data set, generating new variables, namely principal components and canonical variates, which provide a simplified version of the sample variance by the generation of fewer but highly explanatory scores at the expense of minimal accuracy loss. Main differences between PCA and CVA techniques stem from the a priori knowledge required by CVA on group membership, in order to be able to minimize intragroup variation while maximizing inter-group variation, which results in a higher degree of separation among groups when compared to PCA analyses. Canonical variables are defined by square distances between the means of the groups obtained by Mahalanobis's D^2 . PCA and CVA analyses were displayed with a 95% confidence interval ellipse. To homogenize the available data and to make statistically valid assumptions samples were bootstrapped 100 times. Multivariate analyses and bootstrapping were performed in R (R Core Team, 2020) using the R library "BiplotGUI" (La Grange et al., 2009).

3.2. Skeletal profiles

In the present study, the standard zooarchaeological units to determine skeletal part abundance have been used: the Number of Identifiable Specimens (NISIP), the Minimum Number of Elements (MNE), the Minimum Number of Individuals (MNI), the Minimum Animal Units (MAU), and its relative frequency (%MAU) (see Lyman and Lyman, 1994).

Due to the high bone fragmentation observed in PTK and the virtual absence of epiphyseal specimens, which allow determining taxa, skeletal part profiles have been analyzed by carcass size according to Bunn's (1982) classification. Small refers to sizes 1 and 2 (up to 120 kg), medium-sized refers to size 3 (ranging from 120 to 450 kg), and large refers to sizes 4 to 6 (exceeding 450 kg). However, to compare with other archaeological sites, such as FLK Zinj or DS, size 3 and 4 carcasses have been merged in a single group. This is justified because only few bone specimens studied here belong to size 4 ($n = 28$). Carcasses have been divided into four anatomical regions: skull (horn, cranium, mandible, and teeth), axial (vertebrae, ribs, pelvis, and scapula), appendicular (limb bones) and compact (carpals, tarsals, patella, phalanges, and sesamoids) bones.

The MNI has been estimated through two methods; first, using maxillary and mandible specimens and isolated teeth, and second, using long limb bones. The first method, as can be seen, offers information about the taxa present at PTK, whereas the second offers a more approximate estimate of carcass MNI. The survivor index (SI) has been applied to evaluate the existent deviation between MNE and MNI values using long limb bones. The survival rate has been obtained as the result of multiplying our MNE value for each skeletal element by the MNE expected given the MNI (obtained from our sample) and dividing it by 100 (Brain, 1969).

To determine the MNE, ribs have been divided following Rodríguez-Hidalgo et al., (2017) system: portion 1 belongs to the epiphysis which includes the head, neck and costal tubercle; portion 2 belongs to the costal angle; portion 3 belongs to the proximal body; portion 4 is composed by the distal body and portion 5 belongs to the sternal zone. The high frequency of fragmentation documented in the PTK's ribs and the lack of landmarks made us determine the rib's MNE through portions 1 and 2. Long limb bones were also divided into upper (humerus and femur), intermediate (radius-ulna and tibia), and lower (metacarpal and metatarsal) limb bones (Domínguez-Rodrigo, 1997a, b). These, in turn, have been divided into proximal and distal epiphysis, proximal shaft, midshaft and distal shaft. The MNE estimates were based on the systematic inclusion of shaft specimens using a manual overlap approach (Yravedra and Domínguez-Rodrigo, 2009), and taking into account the size, side, landmarks, and ontogenetic age of each identifiable specimen (Barba and Domínguez-Rodrigo, 2005). Given that destructive processes like differential preservation, carnivore ravaging, and water flows tend to eliminate or underrepresent less dense bones (e.g., Voorhies, 1969; Brain, 1967, 1969; Lyman, 1984, 1992; Marean and Spencer, 1991; Marean et al., 1992; Capaldo, 1998b; Pickering et al., 2003). %MAU was compared with bone density values. Density values were acquired from Lyman (1982, 1984) for small carcasses and Lam et al. (1999) for medium-sized carcasses. In order to approach the exploitation and transport strategies that took place at PTK, skeletal profiles have been evaluated through the statistical correlation between %MAU and the utility index (Binford, 1978). The modified general utility index (MGUI) for small carcasses has been obtained from Binford (1978), and the standardized food utility index (SFUI) for medium-sized carcasses stems from Metcalfe and Jones (1988). Spearman's correlations were applied first on all skeletal elements and second on the high-survival elements (skull, mandible, and long limb bones). For this latter analysis, the samples

were bootstrapped 1000 times to avoid type II error, as described by Faith et al. (2009), since at PTK the samples are small ($n = 37$ for small size and $n = 77$ for mid-size carcasses). Finally, high-survival elements were used to identify the most probable transport strategy through a uniformity index. Shannon evenness index measures the uniformity of the distribution of skeletal elements concerning a complete carcass. Evenness values between 0.961 and 0.996 suggest a complete carcass transport or no transport while values lower than 0.96 suggest a selective transport if sample sizes are equal or higher than 100 elements (Faith and Gordon, 2007; Egeland et al., 2008). If MNE samples are equal to 50 then the threshold lowers to 0.92 (Faith and Gordon, 2007).

3.3. Testing site integrity

Due to the clear bias documented in the skeletal profiles, we applied a series of statistical analyses targeting specimen size distribution and the shape and composition of the faunal remains, in order to detect the degree of site integrity. Experimental studies have shown that post-depositional processes, such as water flows (e.g., Badgley, 1986a,b; Coard and Dennell, 1995; Domínguez-Rodrigo et al., 2014b; Isaac, 1967; Kreutzer, 1988; Schick, 1984; Toots, 1965; Voorhies, 1969), trampling, or even gravity (Kerbis-Peterhans, 1990; Domínguez-Rodrigo and Martínez-Navarro, 2012; Krajcarz and Krajcarz, 2014) can produce a preferential distribution of major axes of material (anisotropy). All the archaeological specimens with a longitudinal axis (A-axis) at least twice as long as their width (B-axis) were measured with compasses and clinometers to obtain their horizontal (azimuth) and vertical (plunge) orientations. (Voorhies, 1969; Fiorillo, 1991; Alcalá, 1994; Howard, 2007). Measurements were taken along an A-axis that divided the specimen symmetrically along its longitudinal axis since elongated objects tend to orient according to this axis (Toots, 1965; Voorhies, 1969; Domínguez-Rodrigo and García-Pérez, 2013). The uniformity of the archaeological assemblage was statistically evaluated by combining three tests. The Rayleigh test (R) was used to evaluate if the material had a preferential unimodal orientation (Fisher, 1995), and the omnibus Kuiper (V) and Watson (W) tests were further used to determine if the orientation of the archaeological assemblage is bimodal or multimodal (Fisher, 1995) in the likely event of an anisotropic distribution. The three tests were applied in this study using the R library "CircStats" (Lund and Agostinelli, 2018).

It has been shown that the shape and composition of bones influence their transport (e.g., Schick, 1984; Visher, 1969; Reineck and Singh, 1980; Stein, 1987; Domínguez-Rodrigo et al., 2014b). Bone fragments were measured to determine their shape (flat, cube, and tube) and composition (dense or trabecular). Bones were defined as "flat" when the thickness was less than one-third of the width; "cube" when the thickness was greater than one-third of the width, and "tube" when the specimen was from a long bone that preserved the complete shaft section. The bone composition was divided into "dense" if dense tissue represented $>2/3$ of the specimen, and "trabecular" if cancellous bone structure constituted more than one-third of the composition of the bone (following Domínguez-Rodrigo et al., 2014b system). The data obtained from level 22A were compared with two experimental assemblages, which represent "transported" and non-transported "lag" samples, and with an ethnoarchaeological assemblage without hydraulic disturbance ("Maasai Camp") (Domínguez-Rodrigo et al., 2014b; Domínguez-Rodrigo and Lezana, 1996). Data were treated statistically using Bootstrapped Confidence Regions for Correspondence Analysis (Ringrose, 2012). This was done with the R "caboot" library (Ringrose, 2019), which performs correspondence analysis on a two-way contingency table and produces bootstrap-based elliptical

confidence regions around the projected coordinates for the categories.

3.4. Bone surface modifications

As mentioned earlier, bone surface modification (BSM) analysis (especially cut marks) is the best method to discern the type of carcass access. Cortical surface preservation was evaluated by taking into consideration the stages of subaerial exposure (Behrensmeyer, 1978) and water-induced modification (Cáceres, 2002). Cortical surfaces were examined with 10–20x hand lenses under a strong oblique light source (Blumenschine, 1995). Several types of marks could be identified: cut marks, percussion marks, tooth marks, trampling, abrasion/polish, and biochemical marks. The analysis applies a “configurational approach” where mark morphology, the anatomical placement of marks, and the sedimentary context of the specimen are taken into account (Fisher, 1995; Pickering and Wallis, 1997; Pickering et al., 2005; 2004; Domínguez-Rodrigo et al., 2005). The identification of tooth and percussion marks was made following the diagnostic criteria outlined by Blumenschine (1988, 1995) and Blumenschine and Selvaggio (1988, 1991). Cut marks were identified and tallied following Bunn (1981) and Domínguez-Rodrigo et al. (2007b, 2009, 2010). Since comparisons of archaeological data with modern experimental assemblages involve processes that do not apply to the latter (diagenetic bone breakage or differential bone surface preservation), long bone mark frequencies were corrected following Pickering et al. (2008) method. This method attempts to correct for both the inflation of specimen frequency through dry breakage and artificial reduction of mark frequencies on poorly preserved cortical surfaces.

A multiple discriminant analysis (MDA) was conducted on the well preserved and dry breakage corrected sample to evaluate BSM information. MDA differentiates among distinct experimental groups (which represent primary or secondary access) and classified the PTK data accordingly (Domínguez-Rodrigo et al., 2014c). Prior to statistical analysis, samples were bootstrapped (1000 replications, with replacement), to normalize sample distribution, a prerequisite to applying standard parametric tests such as MDA. The statistical analysis was performed in the R software (R Core Team, 2020) using the R library “BiplotGUI” (La Grange et al., 2009).

3.5. Bone breakage patterns

Earlier studies documenting that the bone breakage producing by dynamic (hammerstone percussion) and static (tooth pressure) loading generate different breakage planes and notches (Capaldo and Blumenschine, 1994; Pickering et al., 2005; Alcántara-García et al., 2006; Domínguez-Rodrigo et al., 2007b; Moclán and Domínguez-Rodrigo, 2018; Moclán et al., 2019).

The analysis of the breakage planes at PTK is based on the identification of green and dry breakage planes following Villa and Mahieu's (1991) criteria and the measurement of the plane angle (longitudinal or oblique relative to the long axis) with a goniometer. Measurements were taken at the point of maximum angle because they represent the extreme values that most of the breakage planes show (see Moclán et al., 2019).

In a previous experimental approximation, Moclán et al. (2019) proposed a method to analyse bone breakage of medium-sized animals produced by carnivores (hyenas and wolves) and direct anthropic percussion based on machine learning techniques (for more information about the experimental samples see Moclán et al., 2019). This approximation combines variables related to the type and the angle (in degrees) of green fracture planes, the length of the specimens, and the presence or absence of epiphyses and

notches (types A, C and D). The analyses proposed by Moclán et al. (2020) are based on the idea that longitudinal and oblique fracture planes (and planes $<90^\circ$ and $>90^\circ$) could be analyzed separately and jointly creating five different types of analyses (i.e., all fracture planes, longitudinal $<90^\circ$ and $>90^\circ$ and oblique $<90^\circ$ and $>90^\circ$).

Recently this method has been reviewed by other authors (Yezzi-Woodley et al., 2022) which have pointed out the existence of some problems related to the data curation (especially in the case of the fracture planes broken by wolves) and the structure of the dataset (there are two variables [length of the specimen and length intervals] which can be considered as redundant) of the original work of Moclán et al. (2019). Currently we are trying to improve the data curation of the sample broken by wolves (Moclán and Domínguez-Rodrigo, work in progress). Yezzi-Woodley et al. (2022) also proposed that the inclusion of some fractures planes of the same type documented on the same single bone specimen (e.g., longitudinal $<90^\circ$) could create methodological biases.

Thus, in this work we have implemented the use of these methods excluding the sample produced by wolves and deleting the ‘interval length’ variable (see Moclán et al., 2019). We have also discarded the use of some fracture planes of the same type observed on the same bone specimen. If there is more than one per specimen, we have only used the most extreme values (i.e., lowest values in the case of $<90^\circ$ and highest in the case of $>90^\circ$) to perform the analyses. In addition, analyses were performed without considering the size of the fracture plane (>4 cm or <4 cm) variable that was included in Moclán's et al., works (2019, 2020), because this variable was not collected during the taphonomic analysis of PTK.

Here we have used five mathematically different algorithms in order to classify the experimental samples of fracture planes broken by hyenas and anthropic percussion: neural networks (NNET), radial kernel support vector machines (SVM), k-nearest neighbours (kNN), random forest (RF) and naïve Bayes (NB). Then, we used the best models (which showed the most accurate results following kappa and accuracy indexes) to classify the fracture planes of PTK. All these algorithms were trained using 70% of the samples as training, and 30% as testing. Cross-validation (10 folds, 10 repeats) was also used. In addition, 10 different configurations of the hyperparameters of the algorithms were used with the function ‘tuneLength’ of the ‘caret’ library of R (Kuhn et al., 2020) in order to define the most accurate model per analysis. As the samples were clearly unbalanced, we used the function ‘upSample’ to overcome the possible bias produced by the data structure. In the original works of Moclán et al. (2019, 2020) bootstrapping was used, here we have only use the upsampling method to create balanced samples. We have also noted which cases have been classified with a probability higher than 0.9 because of the reliability in how they can be considered as true positives.

As can be seen in Table S3 some algorithms have provided kappa values which can be considered as valid (i.e., >0.4) to classify the archaeological samples. These algorithms are NNET and RF for all the fracture planes, NNET, kNN and NB for longitudinal fracture planes $<90^\circ$, NNET for longitudinal fracture planes $>90^\circ$ and NNET for oblique fracture planes $>90^\circ$. In this sense, we have discarded the use of the oblique fracture planes $<90^\circ$ to classify the archaeological samples (instead of they are included in the analysis of ‘all fracture planes’).

Fracture notches were identified according to the typological classification proposed by Pickering and Egeland (2006) (modified from Capaldo and Blumenschine, 1994): 1) complete notches (Type A) have two inflection points on the cortical surfaces and a non-overlapping negative flake scar; 2) incomplete notches (Type B) are missing one of the inflection points; 3) double overlapping notches (Type C) have negative flake scars that overlap with an

adjacent notch; 4) double opposing complete notches (type D) are two notches that appear on opposite sides of a fragment and result from two opposing loading points; and 5), micro notches (Type E, <1 cm).

Bootstrapped Correspondence Analysis (Moclán and Domínguez-Rodrigo, 2018) was used to identify the more probable agent that produced the notch assemblage in PTK. This approximation allows for comparison of the notches present on PTK small and medium-sized animals with those generated by anthropic percussion (Blasco et al., 2014; de Juana and Domínguez-Rodrigo, 2011; Moclán and Domínguez-Rodrigo, 2018), anthropic battering (Blasco et al., 2014) the activity of hyenas (Domínguez-Rodrigo et al., 2007b), and lions (Arráiz et al., 2017). The analysis was performed using the 'cabotcrs' R library (Ringrose, 2019).

Shaft circumference type frequency provides information about the agent of breakage (Bunn, 1982, 1983) and the integrity of a site (Marean et al., 2004; Pickering and Egeland, 2006). Based on data from experimental hammerstone-broken assemblages and hyena dens, three types of shaft circumference were established following Bunn's (1982) classification: Type 1 fragments retain <50% of the original circumference, Type 2 retain >50% and Type 3 preserve the complete shaft circumference.

In order to evaluate the degree of ravaging intensity at PTK, the indices proposed by Domínguez-Rodrigo and Organista (2007) were used: 1) the ratio of axial to appendicular remains, and 2) the ratio of proximal humerus and distal radius to distal humerus and proximal radius. Since the assemblage was broken mostly by hominins, the ratio of femur to tibia was excluded from the analysis. The values of these ratios classify the assemblage into one of the four different ravaging stages being stage 0 indicative of non-ravaging and stage 4 complete ravaging. Indeterminate axial and appendicular specimens were not taken into account in the calculations.

4. Results

4.1. Age profiles

The MNI determined by teeth, including isolated teeth, from mandibles and maxillae is 20. Of these individuals, 15 are bovids, and the other five belong to *Equus*, *Hippopotamus*, *suidae*, *Theropithecus*, and *Homo habilis*. We focused on the age at death of the bovids and the equid. The small carcasses are represented by three individuals: two prime adults and one old individual (Table 1). Medium-sized carcasses are represented by 13 individuals: two young juveniles, three subadult juveniles, seven prime adults and one old individual (Table 1).

Considering the postcranial skeleton, the MNI is slightly higher. For small carcasses, it has been estimated at 10 by the humerus. We documented nine left caudal distal shaft specimens; one belongs to an adult individual (size 1) and eight to subadult individuals of carcass sizes 1 (n = 4) and 2 (n = 4). Right humeri have been quantified by two distal shafts from adult individuals, but one of them could be the antimeres of an adult left humerus, and the other belongs to a size 2 carcass. Regarding medium-sized carcasses, the MNI of 11 has been determined by both femoral and tibial elements. In the first case, the femora are composed of 10 right caudal shafts (three of them belong to juvenile animals) and one left caudal distal shaft with a very thick cortical section. In the case of the tibia, eight left caudal-lateral proximal shafts with the presence of foramina and one shaft belonging to *Equus* have been documented. The left tibiae are represented by two cranial proximal shafts which were still in the growing process. The long bone cortex growth patterns show the typical fibrolamellar bone tissue (highly vascularized) during subadult age growing into dense periosteal

Table 1

A) Minimum number of individuals represented at PTK level 22A by teeth elements. B) Minimum number of bovids and equids represented by teeth elements, postcranial elements and teeth plus postcranial elements.

A Taxa	MNI teeth			
	young juvenile	subadult juvenile	prime adult	old adult
Antilopini			1	
<i>Antidorcas recki</i>			1	1
<i>Kobus sigmoidalis</i>	2	2	2	1
<i>Parmularius altidens</i>			2	
Alcelaphini			2	
Hipotragini			1	
<i>Equus</i> sp		1		
Suidae			1	
<i>Hippopotamus</i> sp			1	
<i>Theropithecus</i>			1	
<i>Homo habilis</i>			1	

B	MNI teeth			MNI postcranial		MNI Post + teeth		
	Juv	Prime	Old	Juv	Adult	Juv	Prime	Old
Size 1-2	0	2	1	8 ^a	2	4	2	1
Size 3-4	5	7	1	3	8	8 ^b	8	1
Total MNI	16			21		24		

^a Include four individuals' size 2 that probably belong to *Kobus sigmoidalis*.

^b Include the four *Kobus sigmoidalis* catalogued as size 2 in the postcranial MNI, one equus and three bovids.

and endosteal lamellar bone in adult age (Manily et al., 2013). According to Carter et al. (1976), bovine long bones are fully grown in about 2 years. If we quantify the elements with woven fibrous bone and less dense as juveniles (young and/or subadult juveniles) their MNI is 11: eight belong to small carcasses and three to medium-sized carcasses. Four of these small carcasses probably belong to juvenile *Kobus* which as adult is a size 3 animal, and were therefore included as medium-sized carcasses in the mortality profiles, since aging is different from taphonomic analysis in carcass size information.

At PTK, DS and Kanjera, the small carcass mortality profiles include more juvenile individuals than FLK Zinj, which is dominated by older individuals. PTK (like DS and Kanjera) falls in the attritional area (using Stiner's model), with a clear trend toward young individuals (Fig. 4A). The mortality profile for medium-sized carcasses falls in the middle of the attritional and catastrophic area (Fig. 4B). Its confidence interval includes all the samples except the lions and hyenas suggesting that the profile is closer to ethnographic and archaeological samples with ambush behaviors. However, due to the archaeological samples being too small, the large confidence ellipses in the ternary diagram cover all carnivore samples being statistically indistinguishable. Taking into consideration the ternary model produced by Discamps and Costamagno (2015) both samples fall into the JPO zone (juvenile, prime, old) which indicates that both samples are dominated by juvenile individuals and could represent both types of profile: attritional or catastrophic. To avoid this equifinality we resort to PCA and CVA analyses using a multiple-age variable partition.

Fig. 5 shows the biplots of the PCA and the CVA analyses which produce three different groups for small-sized carcasses. The first group is formed by FLK Zinj, which appears separate and close to prime-adult dominated individuals. The second group is composed of the lion and hyena samples and DS and PTK archaeological samples which are slightly overlapping with them, suggesting an ambush hunting strategy. The third group includes the cursorial samples from wild dogs and leopards, the ethnographic sample of Hadza and the archaeological site of Kanjera.

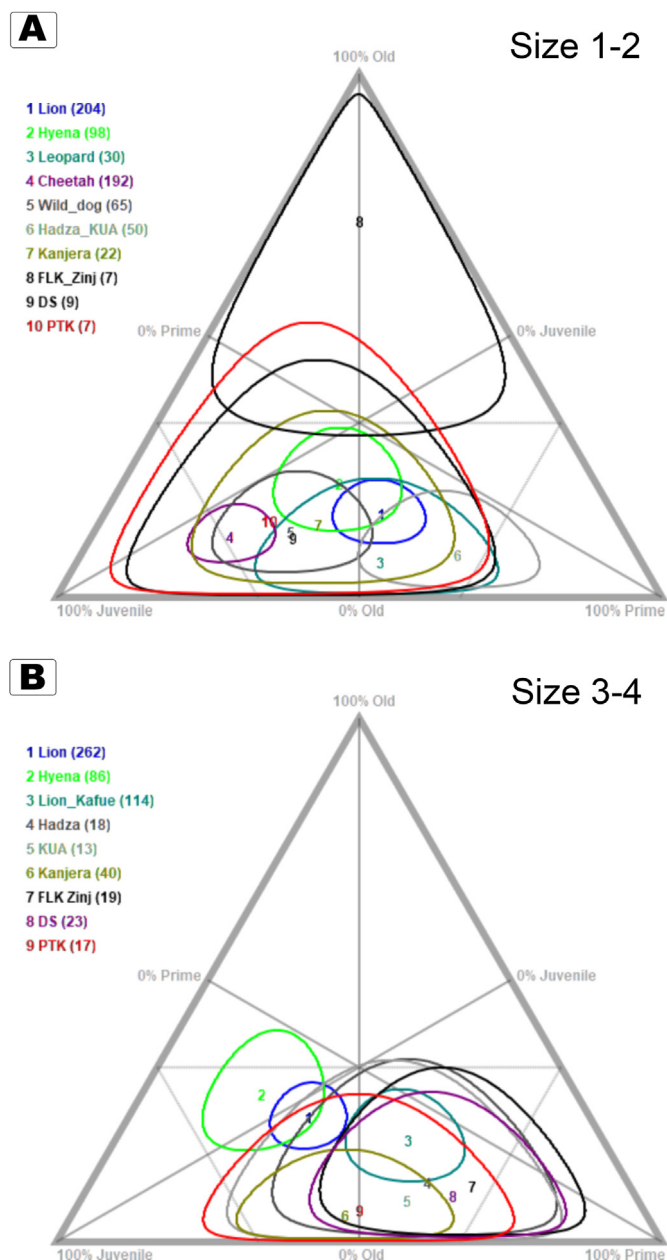


Fig. 4. Triangle graphs showing the mortality patterns for small and medium-sized bovids killed by lions, hyenas, cheetahs, leopards, wild dogs, and Hadza and Kua hunter-gatherers, as well as the mortality profiles documented at PTK, Kanjera, DS, and FLK Zinj.

The PCA and CVA biplots also show three different groups for medium-sized carcasses (Fig. 6). The first group is formed by FLK Zinj and DS; both archaeological sites appear close to prime-adult dominated individuals. Their location and their separation from other samples, as Cobo-Sánchez (2020) indicates, is probably because they reflect a hominin-specific carcass-acquisition (hunting) model (Bunn and Pickering, 2010; Domínguez-Rodrigo and Pickering, 2017). The second group comprises the lion and hyena samples. The third group includes the ethnographic samples and the archaeological sites of Kanjera and PTK, which show a bias toward juvenile individuals suggesting a cursorial hunting strategy

if the agency was a nonhominin carnivoran. The wild dog prey mortality pattern resembles that of ethnographic samples and it slightly overlaps with them.

Given the closed-vegetation environment surrounding the PTK-DS-FLK Zinj sites (Arráiz et al., 2017), we argue that hominins may have employed an ambush strategy to acquire small and medium-sized carcasses (Bunn and Gurtov, 2014). However, this may have differed from mammal carnivore ambush strategies in that the latter produce a more eclectic age profiles, since it is non-discriminatory and it samples age distribution in the prey species cohort demographics (Bunn and Gurtov, 2014), whereas hominin ambush strategy at PTK may have been more selective, targeting juvenile and prime adults over the rest of potential age profiles.

4.2. Skeletal profiles

As explained above, the MNI differs depending on whether only teeth or teeth plus long bones are used (Table 1). The faunal assemblage is composed of 1265 specimens out of which 344 (27%) belong to small carcasses, 786 (62%) belong to medium-sized carcasses and 143 (11%) could not be assigned to carcass size. Tables 2 and 3 show the NISP and MNE per element for each carcass size. Correlations between NISP and MNE for small and medium-sized carcasses result in significant and high correlation coefficients (Spearman's rho = 0.8) in both samples.

Small animals are mainly represented by long bones, mandibles and pelvis (Fig. 7). Long limb bones constitute 40% (n = 139) of the sample, with the humerus being represented almost twice as much as the rest of the long limb bones. Axial elements, such as ribs, vertebrae, and scapulae are underrepresented, as measured by MNE and MNI. Compact bones (carpals, tarsals, and phalanges), and long bone epiphyses are almost absent (n = 13) (Fig. 8). Proximal epiphyses from the radius-ulna are the best represented followed by both epiphyses from humeri, while femoral and tibial epiphyses are missing. Only two distal epiphyses from tibiae were recovered, one of them digested. Medium-sized carcasses show a similar pattern of skeletal abundance (Fig. 7). Axial and compact bones are underrepresented. Long bones are most frequently represented by shaft portions (n = 407; 52%) while the epiphyses are underrepresented (n = 24), and they mainly belong to metapodials (n = 14; 58%) (Fig. 9). Table S4 shows skeletal element abundances in Minimum Number of Elements (MNE) and Percent Minimal Animal Units (%MAU).

As a consequence of the low level of cancellous bone representation, the attrition effects were estimated through Spearman's rank-order correlations between %MAU and bone mineral density (Table 4). Taking into account that most of the small carcasses belong to juvenile animals, the correlations between %MAU and bone density are only approximate. The coefficients show a significant correlation for medium-sized carcasses, but not so for small carcasses. Considering the high-survival element subsample, the correlation coefficients are negative, showing an inverted relationship for small and medium carcasses.

When analysing the skeletal parts according to food utility indexes, the results are non-significant in both carcass size groups (Table 4). Considering the high-survival bootstrapped subsample the results are similar for small carcasses, whereas medium-sized carcasses show a significant but weak correlation. According to these results and taking into account that the MNE samples are lower than 50 for small and lower than 100 for medium carcasses, the evenness index (Table 4), suggests that small and medium-sized carcasses may have been transported complete to the site

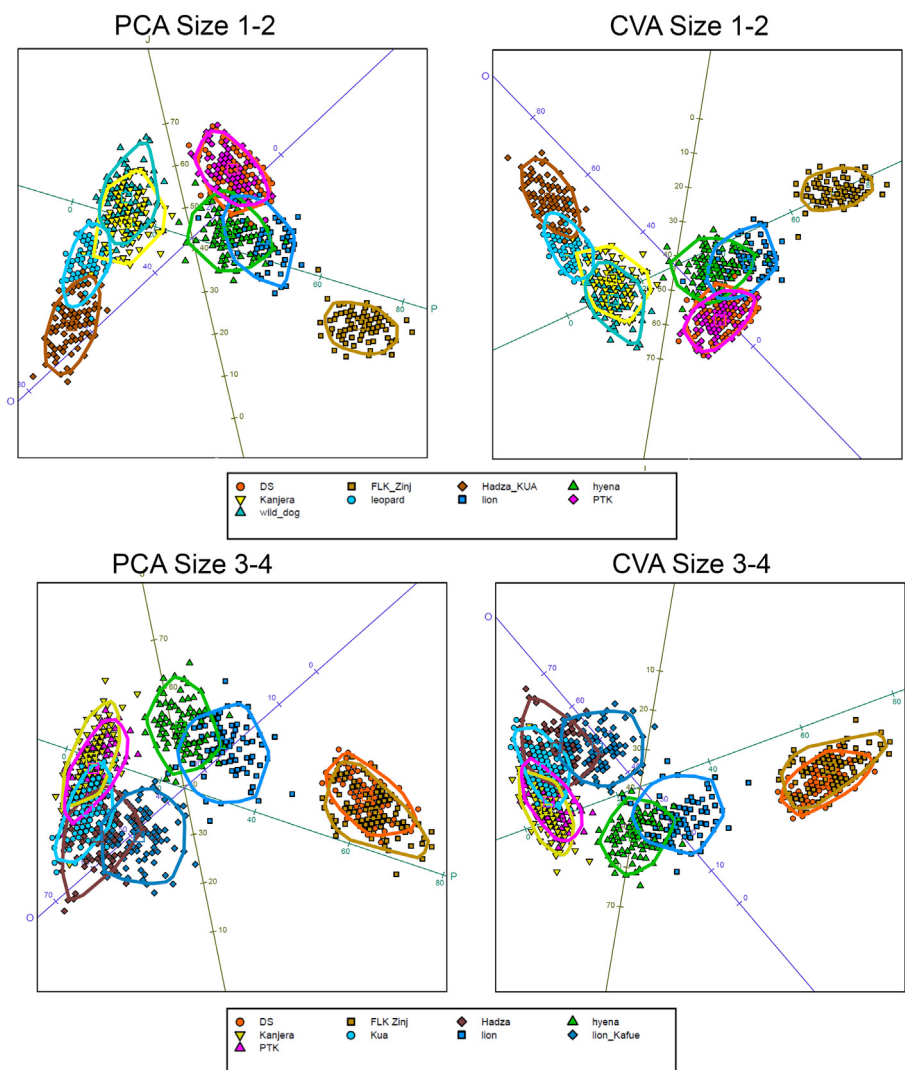


Fig. 5. Multiple discriminant analysis using A) Principal Component Analysis (PCA) and B) Canonical Variate Analysis on the bootstrapped samples of the mortality profiles generated by carnivores and modern hunter-gatherers, as well as the age profiles documented at PTK (current study), DS (Cobo-Sánchez, 2020), FLK Zinj (Bunn and Pickering, 2010) and Kanjera (Oliver et al., 2019), regarding small bovids and using three age classes.

(or unselected), since their confidence interval values are within the 95% confidence limits of even element representation (0.92–0.99 see Faith and Gordon, 2007).

4.3. Testing site integrity

The documented underrepresentation of cancellous bones suggests that abiotic and/or biotic agents acted in the PTK faunal assemblage. Hydraulic flows easily transport the small and low-density elements. This would explain in part why most cancellous elements and portions are highly underrepresented. However, the analysis on specimen length distribution shows that the fragments between 21 and 40 mm are the most abundant ones, and that, in general, frequencies decrease until reaching specimens >100 mm. This pattern is echoed in the sub-sample of green-broken long bone specimens (Fig. 10A). The high frequency of very small specimens and the low frequency of polished and rolled specimens ($n = 49$), the majority of them in 1st degree ($n = 37$) and the rest in 2nd degree, according to Cáceres (2002) system, indicate a limited post-depositional disturbance by abiotic factors (Fig. 10B). In addition, the analysis on bone shape and composition locates PTK next to the

experimentally undisturbed assemblage (Maasai Camp), indicating that PTK is an assemblage without significant hydraulic disturbance (Fig. 10C and Table S5). This statement is corroborated by circular statistical tests, which reflect an autochthonous uniform distribution of the stone tools and fossil bones ($R = 0.888$, $p = 0.412$; $V = 1.946$, $p = <0.02$; $U2 = 0.135$, $p = >0.1$). Additionally, the clustering of long limb shaft fragments according to element (i.e., fragments from the same type of bone occur concentrated in the same *loci*), indicates that the site represents the original depositional locus, and that post-depositional disturbance only scattered few shaft fragments in the vicinity of their concentration (Fig. 11).

4.4. Bone surface modifications

Once the hydraulic flows were discarded as an important factor explaining bone deletion from the PTK archaeofaunal assemblage, focus was placed on BSM and the attrition produced by biotic agents. In general, all bone material is well preserved: 68% of the sample shows good cortical preservation, with the majority of the specimens showing a stage 0 and 1 (58% and 28%, respectively) of subaerial exposition, suggesting that the assemblage was quickly

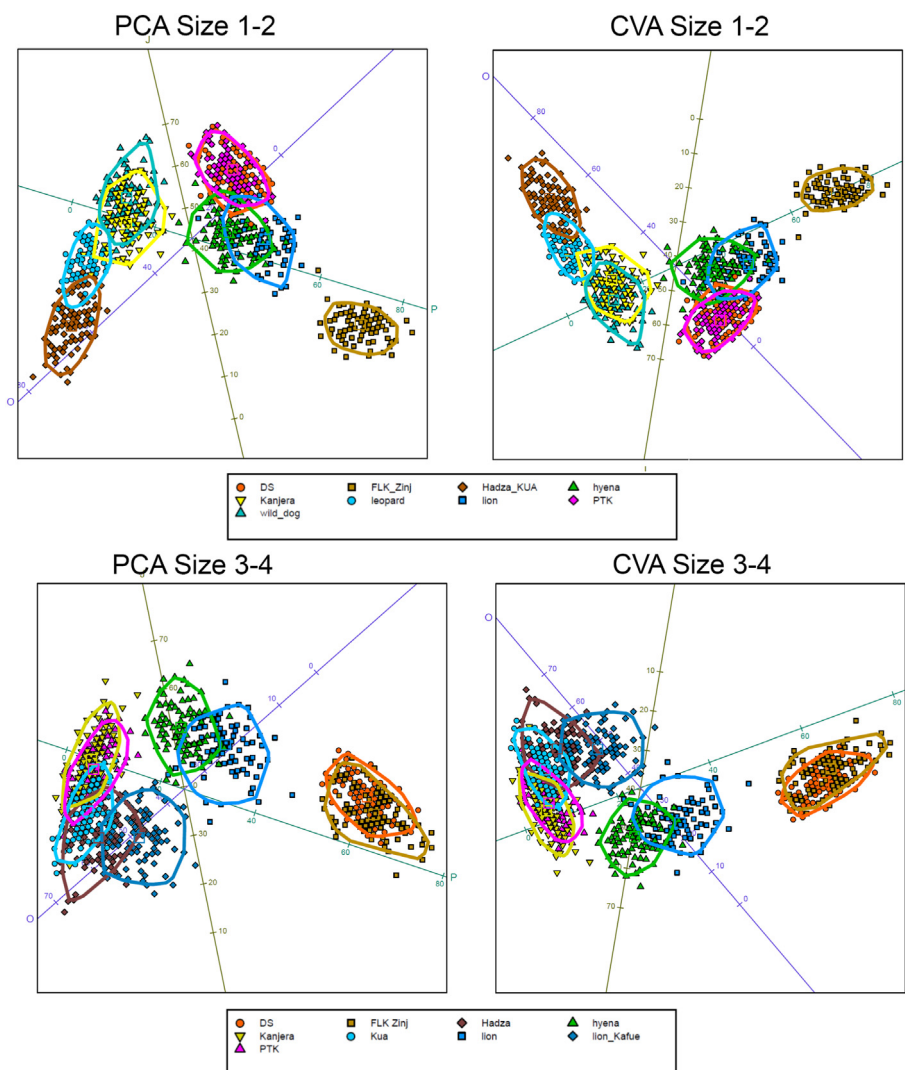


Fig. 6. Multiple discriminant analysis using A) Principal Component Analysis (PCA) and B) Canonical Variate Analysis on the bootstrapped samples of the mortality profiles generated by carnivores and modern hunter-gatherers, as well as the age profiles documented at PTK (current study), DS (Cobo-Sánchez, 2020), FLK Zinj (Bunn and Pickering, 2010) and Kanjera (Oliver et al., 2019), regarding medium bovids and using three age classes.

buried after deposition and that the site formed during a short time span. The preservation of original cortical surfaces allowed us to examine if alteration of the outer cortical layer was caused by subaerial weathering or chemical weathering during diagenesis. At PTK, most of the cortical modification is of chemical origin.

The low representation of axial elements and epiphyses suggests intense carnivore ravaging or other density mediated destruction processes that do not include water flows. However, a low frequency of tooth-marked specimens ($n = 9$ for small carcasses and $n = 28$ for medium carcasses) has been documented. Carnivore damage is mainly documented on long limb bones (77% and 78% of all documented tooth marks respectively according to carcass size) (Tables 2 and 3). Cut mark frequencies on the NISP are moderate, with 6% of small-sized identified specimens and 9% of medium-sized identified specimens presenting cut marks. The majority of the cut marks occur on midshaft sections of long limb bones: 55% and 52% of the total cut marks observed on small and medium-sized identified carcasses appear on long bone midshaft. ULB and ILB display the highest frequencies of cut marks (Table 5).

The BSM frequencies documented on the corrected long limb bone sub-sample are shown in Table 6 and show that 12.9% of

small-sized long bone midshafts bear cut-marks, and the percentage is 17% among medium-sized carcasses (Fig. 12). The low percentage of tooth marks and the higher percentage of cut-marked long bone specimens occur mainly on hot zones (which are areas on limb bones where flesh scraps rarely survive after lion consumption) (Figs. S1 and S2). This confirms that the assemblage was produced and exploited first by hominins, who consumed the flesh and extracted the bone marrow (see below). Cut marks were also identified on cranial, mandibular, and axial bones, including scapulae and pelvis (Tables 2 and 3), which also confirms that hominins had primary access to bulk flesh from whole carcasses and exploited them intensively. This is supported by the predominance of juvenile individuals, which would be utterly defleshed had hominins acquired them after felids initiated consumption (Cavallo and Blumenshine, 1989; Stiner, 1990, 1991; Domínguez-Rodrigo, 2001). Cut marks have been also detected on two phalanges belonging to small-sized animals, being one of them on a juvenile individual, suggests that hominins could also be skinning the animals (Fig. 12). Finally, the MDA analysis locates PTK within the experimental model of primary access more than secondary access (Fig. 13 and Table S6).

Table 2

Skeletal part profiles of small size (size 1–2) carcasses at PTK level 22A. NISP, number of identified specimens; MNE, Minimum number of elements; TM, tooth marked specimens; PM, hammerstone-percussed specimens; CM, cut marked specimens.

Element	NISP	MNE	TM	PM	CM
Skull	9	2			
Hemimandible	14	4			1
Teeth	19	0			
Vertebrae					
Atlas	0	0			
Axis	0	0			
Cervical	3	3			
Thoracic	5	5			
Lumbar	2	1			
Sacra	0	0			
Caudal	0	0			
Indet	8	4			
Ribs	111	20	1		6
Scapula	3	2			
Innominate	13	3			
Sacro	1	1	1		
Humerus		11			
EP	2				
SH	28		1	2	5
ED	2		1		
Radius-Ulna		5			
EP	4		1		
SH	17		1		3
ED	0				
Metacarpal		5			
EP	1				
SH	8				
ED	2			1	
Femur		4			
EP	0				
SH	14			1	2
ED	0				
Tibia		3			
EP	0				
SH	7				
ED	1				
Metatarsal		3			
EP	1				
SH	4		1		
ED	0				
ULB	12		1	1	1
ILB	4			2	
LLB	4				
Carpals	0	0			
Tarsals	1	1			
Phalanges	7	5			2
Other					
Hyoid	1	1			
Sesamoid	0	0			
Patella	0	0			
Sternum	0	0			
Indet	8				
Indet LB	28		1	1	
Total	344	83	9	8	20

The percentages of percussion marks on long bones are 7% for small carcasses and 16.1% for medium-sized carcasses (Fig. 14). The lower percentage of percussion marks on small carcasses may be explained by the fact that most of them belong to juvenile individuals and they do not have a fatty marrow because the marrow cavity is composed of red blood cells -red marrow-which is low in fat content (Blumenschine and Madrigal, 1993; Munro and Bar-Oz, 2005; Currey, 2006). Nevertheless, both values fall into the 95-confidence interval of hammerstone to carnivore experimental samples (Blumenschine, 1988, 1995; Capaldo, 1997). Faced with this situation, other intervening carnivores were limited to scavenging the remains abandoned by hominins. Considering that tooth and

Table 3

Skeletal part profiles of medium-sized (size 3–4) carcasses at PTK level 22A. NISP, number of identified specimens; MNE, Minimum number of elements; TM, tooth marked specimens; PM, hammerstone-percussed specimens; CM, cut marked specimens.

Element	NISP	MNE	TM	PM	CM
Skull	20	2			1
Hemimandible	52	7		5	4
Teeth	29				
Vertebrae					
Atlas	0	0			
Axis	0	0			
Cervical	4	3			1
Thoracic	14	5	1		3
Lumbar	11	8			
Sacra	0	0			
Caudal	0	0			
Indet	5	1			1
Ribs	126	19	2		12
Scapula	14	3	2		2
Innominate	15	5	1	3	2
Sacro	0	0			
Humerus		15			
EP	0				
SH	45			6	9
ED	1				
Radius-Ulna		9			
EP	5				
SH	29		2	2	
ED	0				
Metacarpal		7			
EP	6		1	1	
SH	25		3	5	4
ED	4				1
Femur		14			
EP	1				
SH	51		5	9	6
ED	2		1		
Tibia		17			
EP	0				
SH	70		3	17	17
ED	1				
Metatarsal		6			
EP	2				
SH	12		1		
ED	2		1		
ULB	28		1	2	1
ILB	22		1	1	1
LLB	15		1	1	
Carpals	4	4			1
Tarsals	3	3			
Phalanges	16	12			
Other					
Hyoid	1	1			
Sesamoid	6	6			
Patella	1	1			
Sternum	0	0			
Indet	50				1
Indet LB	83		2	4	4
Total	778	148	28	56	71

percussion marks frequencies are low, notches and breakage planes were analyzed to confirm the main agent(s) of bone breakage at PTK.

4.5. Bone breakage patterns

A total of 868 bone specimens could be identified as bearing green and/or dry breakage. Of these, 696 (80.2%) specimens show green breakage only, 100 (11.5%) have dry breakage only, and 72 (8.2%) specimens have both types of breakage. The majority of the green breakage is present on appendicular bones ($n = 483$, 69.4%), with the rest documented on axial ($n = 131$, 18.8%) and cranial

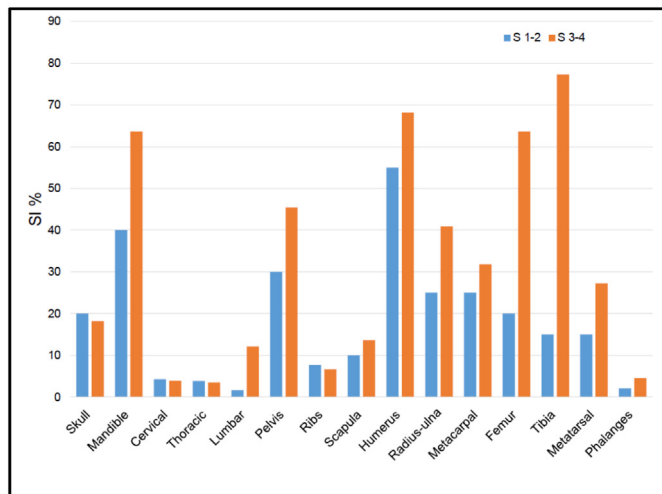
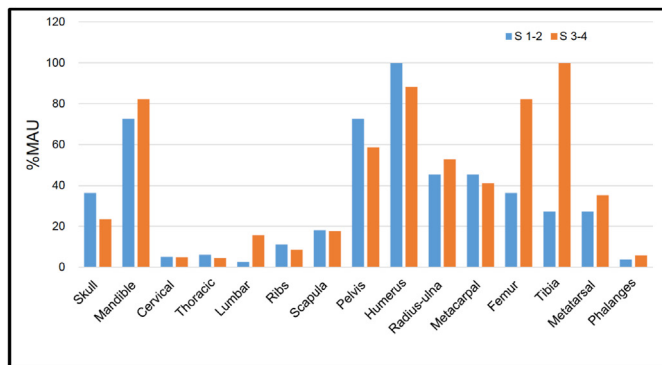


Fig. 7. Skeletal part profiles and survivor index by carcass size.



Fig. 8. Epiphyseal specimens from small carcasses documented at PTK level 22A.

bones (n = 48, 6.9%); the remaining 34 specimens show indeterminate breakage types (4.9%). Dry breakage is documented mostly on axial bones (n = 55, 55%), cranial bones (n = 14, 14%), and more marginally on appendicular bones (n = 10, 10%); the 21 remaining are indeterminate. When analysing breakage type on the long bone subsample only, we studied 532 long bone shaft fragments. Of these, 423 (79.5%) bear green fractures, 10 (1.8%) show dry breaks,



Fig. 9. Epiphyseal specimens from medium carcasses documented at PTK level 22A.

and 50 (9.3%) bear both green and dry fractures. Shaft circumference types show that Type 1 is predominant at 77.6% (n = 413) while Type 2 and Type 3 show lower frequencies: 5.1% (n = 27) and 6.2% (n = 33), respectively. This suggests two things: first, it confirms the integrity of the site, and second, that biotic agents were breaking the bones (Fig. 15).

A total of 64 notches have been identified in the assemblage (Fig. 15). The frequency of the different type notches has shown a greater presence of types B (n = 25) and A (n = 24), followed by types C (n = 11) and D (n = 4). Notches are distributed across all bone types including two hemimandibles and one phalanx, but the majority of the notches are present on long bones. Humeri and femora present the highest number of notches (n = 19 and n = 13, respectively) followed by tibiae (n = 8), radii-ulnae (n = 6), metacarpals (n = 7) and metatarsals (n = 2). Notch type A is the most frequent (43.7%) in ULB followed by notch type B (31.2%).

The analysis of the notches (Fig. 16) shows that there is a clear overlap between the 95% confidence interval of the sample of small carcasses of PTK and the anthropic experimental samples. However, the small sample size provides a very large ellipse that is also overlapping with battering activities and direct percussion. Nevertheless, the mean value of the sample seems to be related to direct percussion activities. In contrast, medium-sized carcasses show a different pattern. This sample clearly overlaps with the notch samples produced by direct percussion, as well as slightly with the one generated by hyenas. Thus, it seems difficult to infer agency from the notch sample. However, a combined model including primary human access and secondary hyena scavenging might be able to explain the patterns observed at PTK, as highlighted by the Correspondence Analysis (Fig. 16).

A total of 218 fracture planes have been measured. Among longitudinal fracture planes 52 fracture planes are <90° and 46 fracture planes are >90°. In the case of the oblique fracture planes, the sample is formed by 57 fracture planes are <90° and 63 fracture planes are >90°.

The new trained models (Table S3) have identified most fracture planes as anthropogenic (Table 7). First, when the analysis is performed using all the fracture planes at the same time (i.e., longitudinal + oblique > and < of 90°) NNET and RF classify 80% and 92.38% of the PTK sample as anthropogenic. These percentages are increased is only those cases classified with probabilities higher than 0.9 are considered, reaching up to 98.33 and 100%.

The results obtained on the longitudinal fracture planes <90° suggest the anthropogenic nature of the assemblage at PTK (between 59,62% and 94,23% of the fracture planes), but in general (with the clear exception of kNN which is the most accurate model

Table 4

Spearman's statistics for the relationship between %MAU – density and %MAU – food utility per carcass size. Skeletal element evenness and 95% confidence limits per carcass size.

%MAU - Density	Size 1-2		Size 3-4	
	Spearman's rho	p-value	Spearman's rho	p-value
Complete skeleton	0.40	0.2	0.68	0.006
High-survival elements (bootstrapped data)	Mean -0.46	p-value <2.2e-16	Mean -0.16	p-value <2.2e-16
%MAU - Food utility	Size 1-2		Size 3-4	
	Spearman's rho	p-value	Spearman's rho	p-value
Complete skeleton	-0.06	0.80	0.08	0.7
High-survival elements (bootstrapped data)	Mean 0.01	p-value 0.10	Mean 0.48	p-value <2.2e-16
Evenness Index	Size 1-2		Size 3-4	
N° high-survival elements	37		77	
Mean	0.91		0.95	
Confidence Interval	0.85-0.96		0.93-0.96	

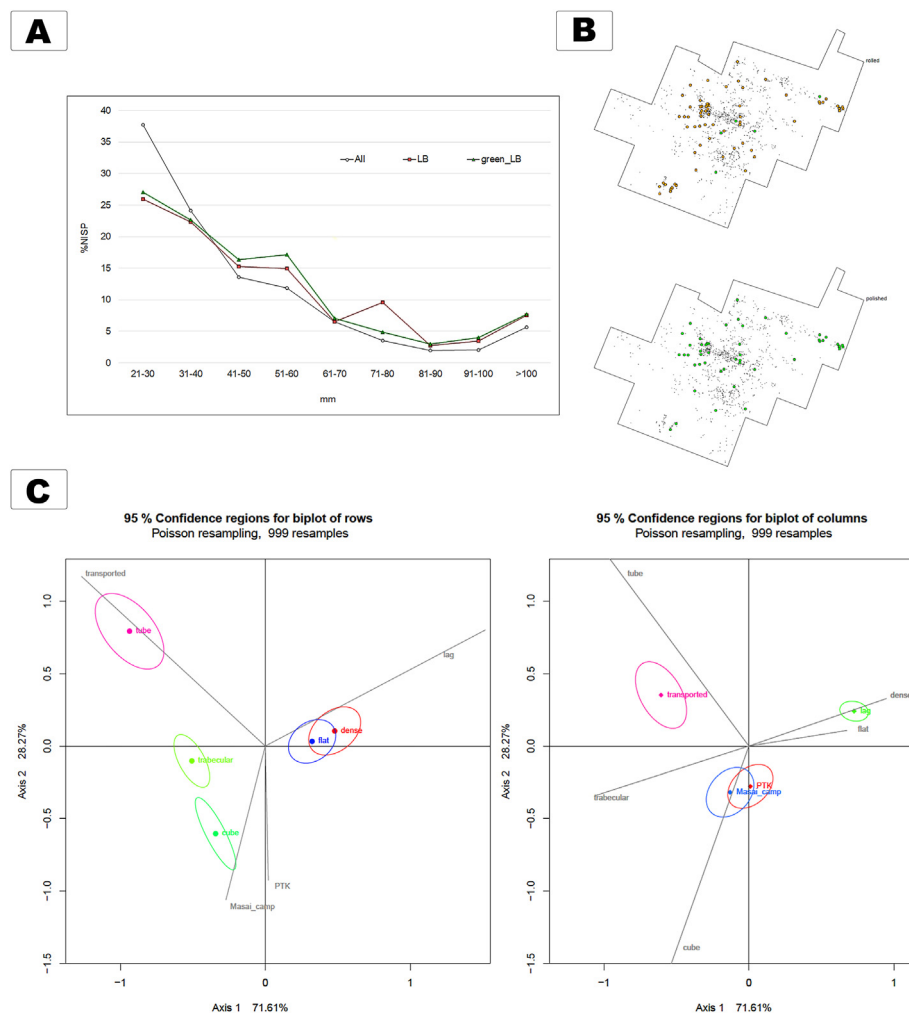


Fig. 10. A) Specimen size distribution quantified by %NISP. B) Distribution of rolled and polished bones at PTK level 22A. C) Biplots of the bootstrapped CA of bones showing the relationship between referential models (Maasai camp, lag and transported modern assemblages) with respect to the shape and composition of bones at PTK level 22A. Data from Domínguez-Rodrigo et al., 2014b. Ellipses with 95% confidence intervals for referential models (left) and shape and composition of bones (right) are also displayed. Length of the axes shows the importance of the contribution of each variable to the inertia. Loading scores for the variables are displayed in Table S5.

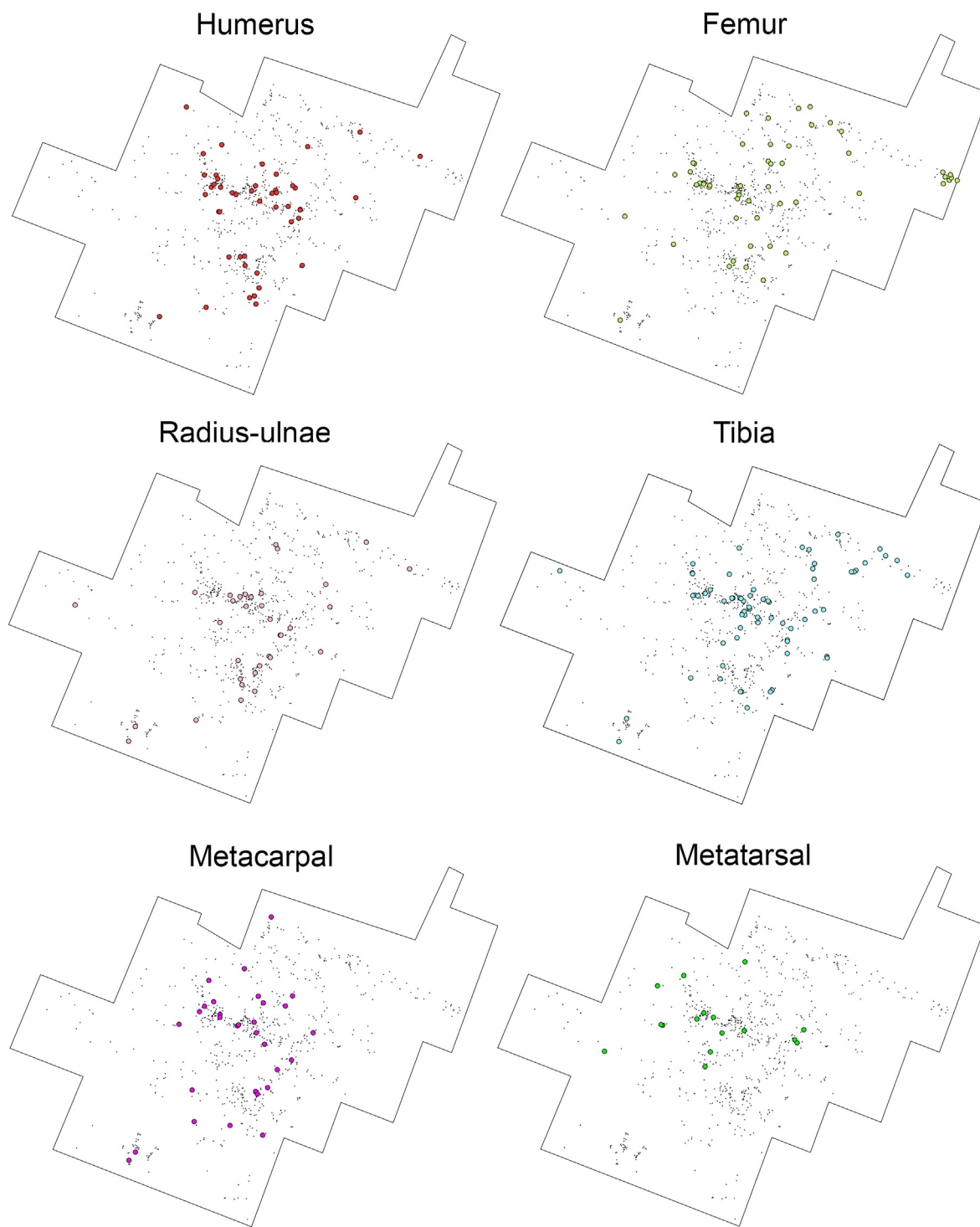


Fig. 11. Spatial distribution of long bones according to element at PTK level 22A.

in this case) the algorithms show a higher number of hyena-broken fracture planes than in the other samples (between 21.15% and the 40,38%). In this case, none fracture plane have been classified with a probability higher than 90%.

In the case of longitudinal fracture planes $>90^\circ$, NNET has classified the most part of the sample as anthropogenic (80.43%) while 5 fracture planes have been identified as anthropogenic with a probability higher than 0.9.

Finally, in the case of oblique fracture planes $>90^\circ$ most of the

fracture planes are also classified as anthropogenic by NNET (92.06%). In this case there are 48 cases classified as anthropogenic with a probability higher than 0.9.

5. Discussion

A previous taphonomic analysis on the cut mark distribution of the zooarchaeological assemblage of PTK concluded that the main accumulation of the sample was produced by anthropogenic

Table 5

Cut mark frequencies per long limb bone and bone section. ULB, upper limb bone; ILB, intermediate limb bone; LLB, lower limb bone; EPI, epiphysis. Numbers in the numerator are total numbers of cut-marked specimens. Numbers in the denominator are the total numbers of specimens. Numbers in parentheses are percentages. * Not included the indeterminate long bone fragments.

	Size 1-2	Size 3-4
ULB	8/58 (14)	16/128 (12.5)
ILB	3/33 (9)	18/127 (14)
LLB	0/20 (0)	5/66 (7.5)
SHAFT*	11/98 (11)	38/297 (13)
EPI	0/13 (0)	1/26 (4)
TOTAL	11/111 (10)	39/323 (12)

activity (Domínguez-Rodrigo et al., 2021). However, that analysis did not address other questions about the processes that created the faunal assemblage final configuration. The taphonomic analysis of PTK that has been detailed in this paper suggests that hominins were processing different animal taxa (e.g., *Antidorcas*, *Kobus*, *Parulanius*, *Hippotragus*) from different ages, with an emphasis on juvenile and prime adult individuals. Bulk flesh and marrow exploitation is supported by the frequency and distribution of cut marks on the high meat-yielding upper and intermediate limb bones and by the frequency of percussion marks on all long limb elements (Figs. 12 and 14). The analysis of breakage planes also confirms that at least between 59,62% and 94,23% of the long bone sample was broken by hominins. Carcasses seem to have been transported in a non-selective way to the site, as the evenness index suggests. Nevertheless, the correlation between %MAU and the density in the small size sample is too small to be significant. The correlation only explains 15% of the sample. From this perspective, complete small carcasses could have been originally transported to the site. This would make more sense vis-a-vis other data, since most of the carcasses are juvenile and easier to transport as complete units (Bunn et al., 1988). In essence, hominins were repeatedly transporting fleshed animal resources into the site, and all taphonomic evidence indicates that these were acquired through primary access (see below).

It must be noted that abiotic processes have produced a low rate of modification of the original biostratigraphic assemblage. However, it is clear that other non-hominin biotic agents modified the original anthropogenic accumulation of carcasses at the site. The use of skeletal profiles to interpret hominin behavior is complex because it is difficult to associate certain skeletal patterns to human activity or specific taphonomic agents. Overall, the skeletal part profiles provide an approximation to interpret hominin carcass transport and exploitation strategies when the anthropogenic agency can be otherwise determined, as well as to evaluate the degree of integrity of the assemblage impacted by taphonomic agents. The PTK's low frequency of axial bones and the high

frequency of limb bones without epiphyseal sections is indicative of post-depositional carnivore ravaging at the site (Capaldo, 1995, 1998; Domínguez-Rodrigo et al., 2015a) rather than the result of a selective transport by hominins. Only 13 long bone specimens display evidence of carnivore gnawing. The hyenid activity on the assemblage is confirmed by the machine learning analysis applied to the breakage planes. Depending on the model and fracture plane, the activity of the hyenas on the assemblage can range from 5,77 to 40,38%. As reported here, the scarcity of epiphyseal sections suggests that bone-crunching hyenas may have deleted these portions after butchery and marrow extraction by hominins. The presence of digested bones (n = 5) belonging to these parts from size 3 juveniles confirms this, and suggests a consecutive use of the site by both hominins and other carnivores. The paucity of tooth marks can also indicate that small carnivores (i.e., jackals) may have intervened by transporting bones away.

When evaluating the degree of ravaging at PTK, the ratio of axial (vertebrae and rib) to long limb bones, and the ratio between proximal humerus plus distal radius to proximal radius plus distal humerus (Fig. 17), the small carcasses value falls inside of stage 2, which represents moderate ravaging, where at least half of the axial and long bones have been reduced by the action of carnivores. While the medium-sized carcasses value is indicative of an intensive carnivore ravaging represented by stage 3, where bones frequencies have been reduced by one-third or less (Domínguez-Rodrigo and Organista, 2007). These stages imply a moderate to high competition habitat. However, the PTK environment was characterized by the presence of trees (Arráiz et al., 2017) that could have served as a refuge by temporarily decreasing the trophic competition (i.e., the timing of access to resources could have been longer than in an open setting, thus lowering the overall competition). Nevertheless, the competition degree also depends on carnivores' nutritional stress. The low representation of migratory animals at PTK, as in FLK Zinj and DS, suggests a dry season occupation (Domínguez-Rodrigo et al., 2019; Linares-Matás and Clark, 2021). The hominin occupation of PTK potentially at the end of the dry season, which is the moment of higher nutritional stress for carnivores, would also explain the potentially higher degree of ravaging or bone deletion) documented in the assemblage.

At PTK, 50% (n = 172) of the small carcass' specimens belong to juvenile animals and 7.5% (n = 13) are cut-marked. The percentage of juvenile specimens belonging to medium-sized carcasses is 21% (n = 167) and 14% of these (n = 24) are cut marked. The predominance of juvenile individuals that preserve a high frequency of cut marks, similar to primary access models (Domínguez-Rodrigo, 1997a), is suggestive of hunting and not of scavenging, since carnivores rapidly destroy small carcasses leaving no remains available for secondary consumers (Schaller, 1968; Blumenschine, 1987; Cavallo and Blumenschine, 1989; Domínguez-Rodrigo, 2001). A similar age pattern has been documented at Kanjera South, Kenya

Table 6

Cut mark, percussion mark and tooth mark frequencies on long bones (LB) and midshaft (MSH) sections per carcass size on corrected sample. Numbers in the numerator are total numbers of marked specimens. Numbers in the denominator are the total numbers of specimens. Numbers in parentheses are percentages.

Sample	NISP	Good preserv.	Green breakage	Dry Breakage	Corrected sample (CS)	CM/CS	PM/CS	TM/CS
Size 1-2 LB	136	101	93	14	100	10/100 (10)	7/100 (7)	3/100 (3)
Size 1-2 MSH	100	75	72	11	77.5	10/77.5 (12.9)	-	1/77.5 (1.3)
Size 3-4 LB	400	238	224	23	235.5	37/235.5 (15.7)	38/235.5 (16.1)	13/235.5 (5.5)
Size 3-4 MSH	273	165	159	17	167.5	28/167.5 (16.7)	-	8/167.5 (4.7)



Fig. 12. Examples of cut-marked bones at PTK level 22A. A) PTK13-346 first phalanx; B) PTK13-550 humerus; C) PTK14-1588 humerus; D) PTK14-1513 femur; E) PTK12-37 femur.

(2.0 Ma) where 50% of the sample belongs to juvenile carcasses, which were also interpreted as having been acquired through hunting (Ferraro et al., 2013; Parkinson, 2013, 2022; Oliver et al., 2019), but with the difference that in Kanjera South the midshaft specimens from size 1 carcasses are not cut-marked while at PTK, the midshaft sample (n = 36) from small size carcasses shows 16%

of cut marks (n = 6). As in Kanjera (Parkinson et al., 2022), a substantial amount of cut marks not only occur on meat-bearing long bones (namely, upper and intermediate elements), but are also located on hot zones where carcasses are usually devoid of scraps if accessed after felids. The juvenile-dominated Kanjera assemblage is probably one of the earliest pieces of evidence of primary access by

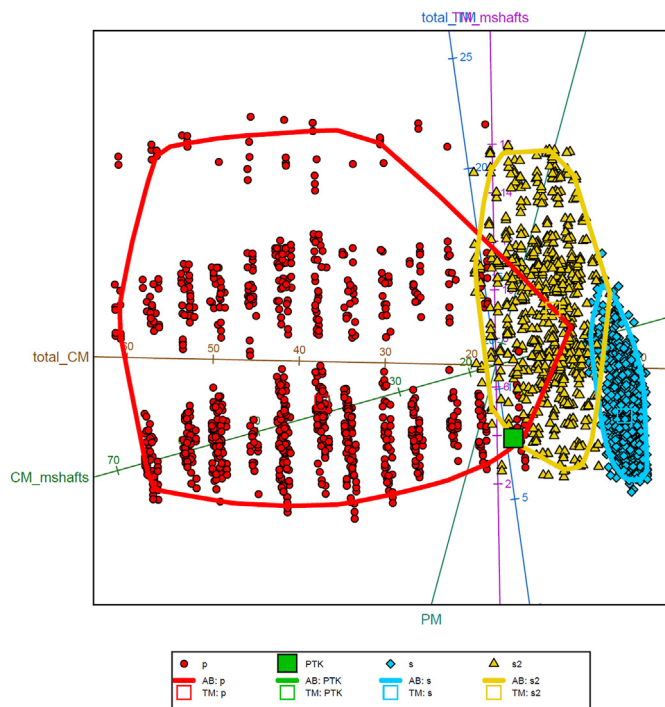


Fig. 13. Multiple discriminant analysis (using a canonical variate approach) on a bootstrapped sample of experimental sets: primary access to completely fleshed carcasses butchered with stone tools reproducing the H–C model (red alpha bag), secondary access to variously defleshed carcasses in the F–H–H model (yellow alpha bag), and secondary access to defleshed carcasses from the F–H model (blue alpha bag). Data from Domínguez-Rodrigo et al. (2014c). Loading scores for the variables are displayed in Table S6. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

hominins, and the pattern of abundance of juveniles and anatomical distribution of cut marks (in higher frequencies) is replicated in the PTK archaeofaunal assemblage.

Oliver et al. (2019) explained the high frequency of juvenile individuals in Kanjera South due to the open paleolandscape of the site, where hominins had to adopt a cursorial strategy to get the most vulnerable prey. In the case of PTK, the paleolandscape is reconstructed on a high lacustrine terrace (UribeArrea et al., 2014), where phytoliths show the presence of forest/palm plants and the presence of ferns suggesting a shaded and humid habitat. PTK would be characterized by mixed paleovegetation, dominated by forest and woodland with patches of open spaces occupied by grasses (Arráiz et al., 2017). In this environment, an ambush strategy seems to be the most appropriate.

At PTK, the carcasses belong mainly to juvenile and adult *Kobus sigmoidalis*. Considering the ethology of the waterbuck, one can speculate about the hunting behavior of hominins. The waterbuck is gregarious and nonmigratory (Foley, 1993). Their territoriality and preference for habitats close to the water with cover and grass (Kiley-Worthington, 1965) could have made them easy to locate. Given that the paleolandscape of PTK responds to these characteristics, it is possible that even hominins and waterbucks shared the same territory. Therefore, it is plausible that prey hunting decisions by early *Homo* were conditioned by the presence of juvenile prey. This could indicate a potential seasonality in the selection of subadults. Ethnographic and ethological studies demonstrate that the seasonal changes and the selection of certain habitats would have profound implications in food-procurement strategies (e.g.,

Speth, 1987; Abraham et al., 2022; Marlowe and Berbesque, 2009; Oelze et al., 2014). Then the selection of juvenile animals at PTK could be in connection with the season (dry or wet), the habitat (resource availability), and prey vulnerability, just as San, !Xo and G/wi hunters of the Kalahari have been observed to do (Schapera, 1965; Liebenberg, 2006). The predominance of prime adult individuals has been seen as the result of the selective ambush strategy (Bunn and Pickering, 2010); however, at the end of the dry season and the beginning of the wet season, the ungulates, and more specifically, the prime adults show higher nutritional stress, which is reflected in a decrease of their fat deposits (Speth, 1987 Tomlinson, 1979, 1981; Murray, 1982; Van Rooyen, 1993). The power struggle to maintain territories results in a substantial decline in adult male body condition (Murray, 1982; Van Rooyen, 1993). Therefore, hominin hunting strategies could have avoided exclusively targeting the prime adult males and focused on other age ranges with more fat-rich resources, such as pregnant females (Linares-Matás and Clark, 2021). This strategy has been documented at FLK Zinj where hominins also targeted fat resources through the acquisition of pregnant females (Bunn and Pickering, 2010). The presence of juveniles, given that the peak of births in waterbucks, as in other antelopes, is documented during the wet season, would be indicative of a dry season occupation. This could also explain the absence of non-local potentially migratory fauna. This situation is coherent with those data provided by the carnivore competition analysis described above.

The comparison of PTK with other pene-contemporaneous sites from Bed I, such as FLK Zinj and DS, shows some differences, but in general, all of these sites represent specific locations selected by hominins on the landscape, with the presence of trees and freshwater resources nearby (Ashley et al., 2010; UribeArrea et al., 2014; Arráiz et al., 2017). Hominins transported fleshed carcasses to these places to be processed and consumed. The three assemblages are represented by similar bovid taxa and by similar proportions of each species. Despite the fact that the three archaeological sites are located in closed-vegetation habitats, and were probably occupied during the dry season (Domínguez-Rodrigo et al., 2019), which should be relatively low-competition habitats (Domínguez-Rodrigo and Organista, 2007), at PTK the carnivore activity seems to be slightly more intensive than at FLK Zinj and DS, where a relatively higher presence of epiphyses has been documented ($n = 166$ from 721 limb bone specimens, 23%; $n = 133$ from 549 limb bone specimens, 24% respectively) as well as more axial elements (Domínguez-Rodrigo and Barba, 2007; Cobo-Sánchez, 2020). The frequency of juvenile individuals at PTK (52%) is higher than at DS (35%) and at FLK Zinj (18.5%). At all the three anthropogenic sites, the juvenile taxa are similar: *Kobus* and *Parmularius*. The selection of young individuals by Oldowan's hominins could be because they may have been more vulnerable and abundant at the end of the dry season. Based on the optimal foraging theory, this strategy could provide them with a higher energy benefit for the lowest cost, maximizing the net energy obtained (Winterhalder, 1981).

It must be noted that PTK also presents a similar size and internal spatial distribution of archaeological materials as documented at FLK Zinj, with most of the assemblage documented in a single spatially-discrete cluster area (Domínguez-Rodrigo and Cobo-Sánchez, 2017a). Inside this discrete area, three peaks of intensity (or sub-clusters) close to one another can be observed (Fig. 3). The similarity to FLK Zinj in the taxonomic composition, amount of materials, skeletal part distribution, taphonomic properties, lithic technology, and spatial distribution indicates a similar hominin behavior at both sites. In this sense, it is probable that the functionality of the site was similar to the one attributed to FLK Zinj



Fig. 14. Examples of percussion-marked tibia shafts at PTK level 22A. A) PTK12-59; B) PTK13-236; C) PTK13-254; D) PTK14-2130; E) PTK14-1900.

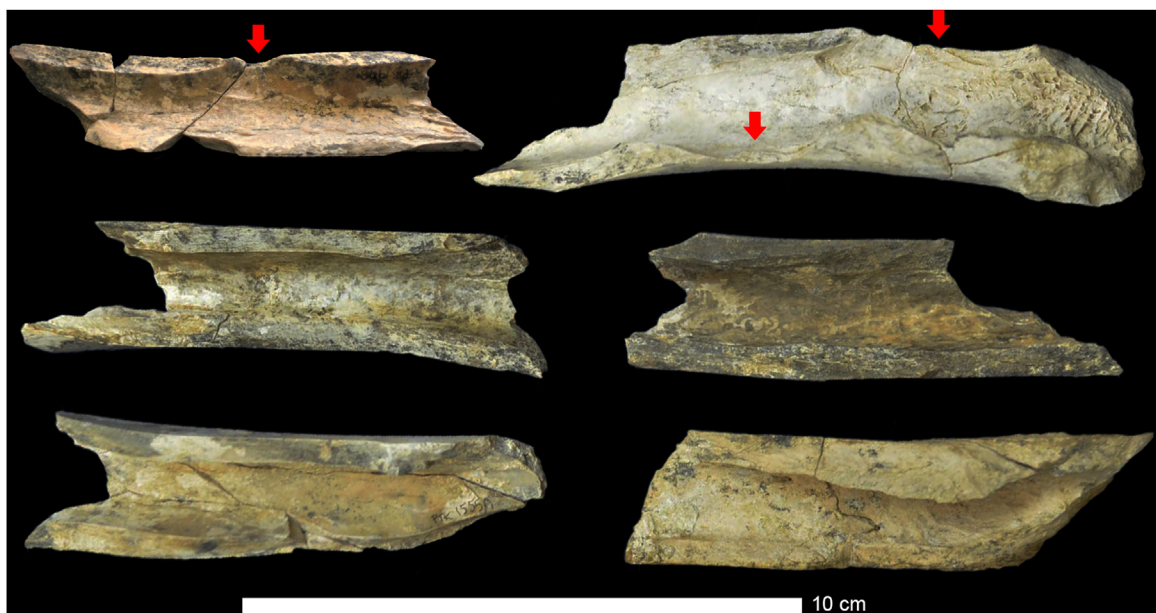


Fig. 15. Several examples of breakage planes on long bone shafts, some of them with notches at PTK level 22A.

(Domínguez-Rodrigo and Cobo-Sánchez, 2017a). Thus, we propose that PTK was used as a central-provisioning place by hominins to where they transported some animal carcasses to be consumed and, probably, shared with other members of the group. PTK also shows the great potential of these nicely preserved archaeological records to unravel cues about the social organization and use of the

space by those early humans, with most carcass consumption repeatedly taking place on the same discrete area, without the typical distribution according to household space that is typical among modern human foragers (Domínguez-Rodrigo and Cobo-Sánchez, 2017b). Future dental microwear analyses at PTK will test the hypothesis that we introduce here about the seasonal

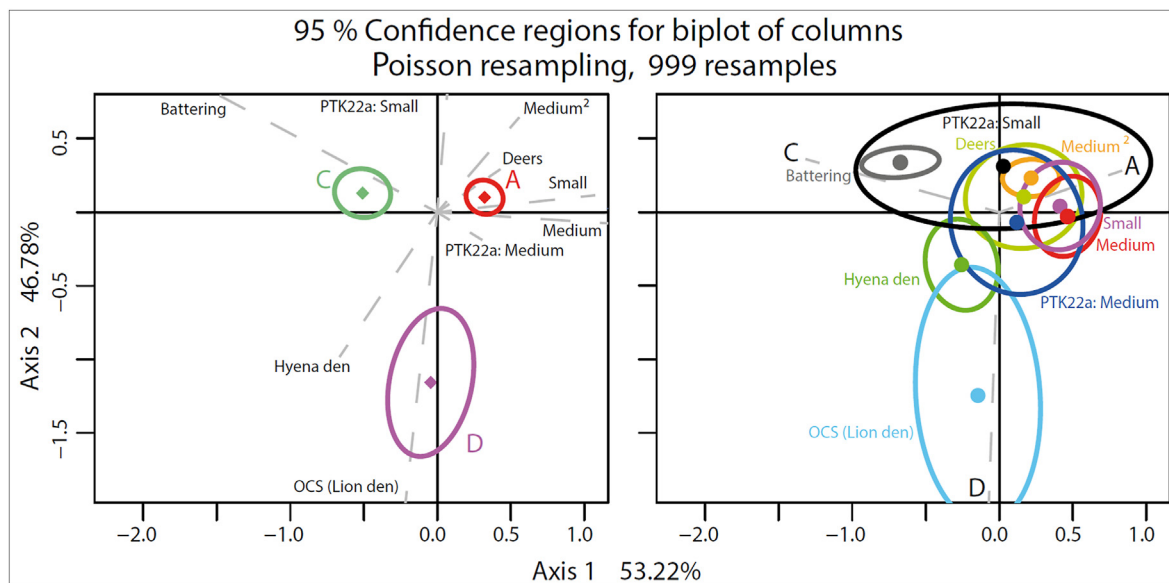


Fig. 16. Biplots of the bootstrapped CA of notch types at PTK showing the relationship between referential models with respect to the notch types at PTK. Ellipses with 95% confidence intervals for referential models (right) and notch types (left) are also displayed. Length of the axes shows the importance of the contribution of each variable to the inertia.

Table 7

Classification of the different bone fracture plane samples with the selected Machine Learning algorithms. In the table, the accuracy and kappa values of the models can be seen. The number of classified PTK fossil specimens per agent (and its percentage) and the number of classified PTK specimens over 90% of confidence ($p > 0.9$) is also shown.

	Accuracy	Kappa	Hyenid	Percussion	Hyenid ($p > 0.9$)	Percussion ($p > 0.9$)
All Fracture planes						
NNET	0.86	0.45	42 (20%)	168 (80%)	1 (1.67%)	59 (98.33%)
RF	0.87	0.41	16 (7.62%)	194 (92.38%)	0 (0%)	104 (100%)
Longitudinal <90°						
NNET	0.7632	0.443	11 (21.15%)	41 (78.85%)	0 (0%)	0 (0%)
kNN	0.8158	0.53	3 (5.77%)	49 (94.23%)	0 (0%)	0 (0%)
NB	0.7368	0.4362	21 (40.38%)	31 (59.62%)	0 (0%)	0 (0%)
Longitudinal >90°						
NNET	0.9322	0.6767	9 (19.57%)	37 (80.43%)	0 (0%)	5 (100%)
Oblique >90°						
NNET	0.939	0.5199	5 (7.94%)	58 (92.06%)	0 (0%)	48 (100%)

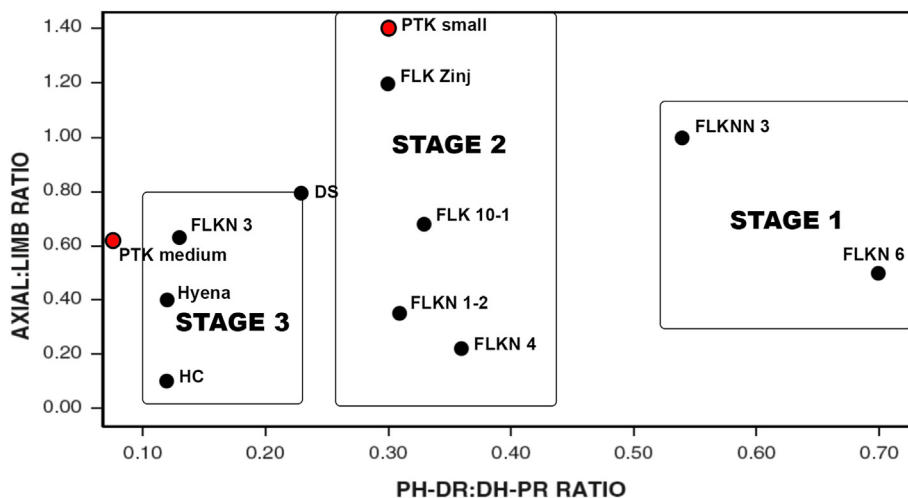


Fig. 17. Ravaging stages of some of the bone assemblages from the Olduvai Bed I sites, using the proximal humerus-distal radius: distal humerus-proximal radius ratio. (Data from hammerstone-to-carnivore experiments (Capaldo, 1995) (HC) and from the Maasai Mara hyena den (Domínguez-Rodrigo et al., 2007b) (Hyena) have also been included for comparison).

nature of the assemblage. Our challenge now is to find the proper models and analogues that make this patterning understandable.

The repeated use of the same loci for food transport, and (presumably) collective consumption, in the absence of fire, would indicate that site selection was determined by low-competition settings, where hominins could engage in food processing, consumption and other activities. This is indicated by the low carnivore input in the immediate paleolandscape surrounding these Bed I sites (Domínguez-Rodrigo et al., 2010). This low-competition condition must have existed at least on a seasonal basis, alternating with higher mammalian carnivore input at other times, where bone remains at these sites were still attractive for durophagous bone-crunching scavengers.

Reconstructions like those provided by the strong anthropogenic signal of sites like PTK, FLK Zinj or DS are not usual and have been referred to as “the Olduvai effect”, implying their anomalous nature (Barr et al., 2022). Some zooarchaeologists seeking longitudinal trends mix chronologically-similar assemblages disregarding if they can be effectively compared (Barr et al., 2022). For such a comparison to be heuristically solid, the basic requirement is to use sites that contain similar qualities in agency and preservation. Most early Pleistocene sites in Africa are affected variously by different degrees of impact by biotic and abiotic processes during their biostratigraphic and diagenetic phases. Comparing sites whose material preservation is deficient, whose integrity is low, and whose study involve different types of taphonomic analyses and methods to sites where hominin agency is prominent and preservation is exceptionally good, biases temporal and behavioral information, and epistemologically flaws interpretations. We argue, contra this approach, that effective longitudinal comparisons can only be made using exceptionally-preserved archaeofaunal records, where hominin behavioral information has been preserved and is minimally biased. This is why sites like PTK contribute to increasing our limited sample of such exceptional records, and documents hominin activities in a degree that other sites impacted by a higher range of taphonomic processes do not.

6. Conclusions

The taphonomic analysis of the PTK faunal assemblage has shown that the site is autochthonous and that it contains a high degree of integrity. The assemblage was formed as a result of the selective transport of fleshed carcasses to the site by hominins who consumed their meat and marrow. After that, hyenid activity was intensive probably deleting a substantial part of the original bone assemblage. The study concludes that the site may have been used by hominins as a central place, where the closed vegetation could have sheltered them from carnivores long enough to allow them to carry out several activities at the site. Its location, near a fluvial input shared with the nearby site of DS, would have enabled hominins to have easy access to water and herbivores using the area as a drinking location. The abundance of young individuals suggests that the hominins in PTK employed a selective hunting strategy slightly different from that documented at FLK Zinj and DS. This analysis reinforces the patterning in prey selection and use documented at other pene-contemporaneous sites, as well as the patterning in the use of the space in these loci by hominins. This clearly has important repercussions in how this information is used to interpret socio-reproductive strategies of early Homo. PTK also contributes to increasing the behavioral range previously documented in other sites, in a time in which the earliest evidence of *Homo aff. Erectus* (using morphological and dimensional criteria) is documented at the gorge (Domínguez-Rodrigo et al., 2015b). The chronologically sympatric co-existence of three hominin taxa (*Paranthropus boisei*, *Homo habilis* and *Homo aff. erectus*) on the

same landscape, one of them with fully terrestrial adaptation, also requires revising the role of *Homo habilis* in the agency of the Oldowan archaeological record at Olduvai Gorge.

Author contributions

EO and AM wrote the main manuscript text. EO, MDR and CPE analyzed the faunal material. EO and AM analyzed the data. LHV restored the faunal material. EO, JA, LCS, DMP, DU, MVR, AG, AM, EB, MDR, collected the archaeological material and reviewed the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

This work was supported by the Swedish Research Council (Vetenskapsrådet) (AR-HS 2018-01045-3). We also thank the Spanish Ministry of Science and Innovation for funding this research (PID 2020-115452 GB-C21), and the Ministry of Culture for their funding through the program of Archaeology Abroad. Our thanks also to the Palarq Foundation and E2in2 for financial support. We additionally thank COSTECH (Commission for Science and Technology), the Division of Antiquities, NCAA (Ngorongoro Conservation Area Authority) and TANAPA (Tanzanian National Parks), within the Tanzanian Ministry of Natural Resources and Tourism for their permission to conduct research in Tanzania. We thank the anonymous reviewers for very helpful comments that clarified our arguments and improved this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2022.107913>.

References

- Abraham, J.O., Hempson, G.P., Faith, J.T., Staver, A.C., 2022. Seasonal strategies differ between tropical and extratropical herbivores. *Journal of Animal Ecology* 91 (3), 681–692.
- Alcalá, L., 1994. *Macromamíferos neógenos de la fosa Alfambra-Teruel*. Instituto de Estudios Turolenses, Zaragoza.
- Alcántara-García, V., Egidio, R.B., del Pino, J.M.B., Ruiz, A.B.C., Vidal, A.I.E., Aparicio, Á.F., Calleja, S.H., Jiménez, A.I., González, M.M., Gil, M.P., Tello, V.P., 2006. Determinación de procesos de fractura sobre huesos frescos: un sistema de análisis de los ángulos de los planos de fracturación como discriminador de agentes bióticos. *Trab. Prehist.* 63 (1), 37–45.
- 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). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 488, 9–20.
- Ashley, G.M., Barboni, D., Domínguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z., Diez-Martin, F., Barba, R., Baquedano, E., 2010. A spring and wooded habitat at FLK Zinj and their relevance to origins of human behavior. *Quat. Res.* 74 (3), 304–314.
- Attwell, C.A.M., 1980. Age determination of the blue wildebeest *Connochaetes taurinus* in Zululand. *S. Afr. J. Zool.* 15 (3), 121–130.
- Badgley, C., 1986a. Taphonomy of mammalian fossil remains from Siwalik rocks of Pakistan. *Paleobiology* 12 (2), 119–142.
- Badgley, C., 1986b. Counting individuals in mammalian fossil assemblages from fluvial environments. *Palaios* 328–338.
- Barr, W.A., Pobiner, B., Rowan, J., Du, A., Faith, J.T., 2022. No sustained increase in

- zoarchaeological evidence for carnivory after the appearance of *Homo erectus*. *Proc. Natl. Acad. Sci. USA* 119 (5).
- Barba, R., Domínguez-Rodrigo, M., 2005. The taphonomic relevance of the analysis of long limb bone shaft features and their application to implement element identification: study of bone thickness and the morphology of the medullary cavity. *Journal of Taphonomy* 3, 111–124.
- Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4 (2), 150–162.
- Binford, L.R., 1978. *Nunamiut Ethnoarchaeology*. Academic Press, New York.
- Binford, L.R., 1981. Bones: Ancient Men and Modern Myths. Academic Press, New York.
- Binford, L.R., 1985. Human ancestors: changing views of their behavior. *J. Anthropol. Archaeol.* 4 (4), 292–327.
- Blasco, R., Domínguez-Rodrigo, M., Arilla, M., Camarós, E., Rosell, J., 2014. Breaking bones to obtain marrow: a comparative study between percussion by batting bone on an anvil and hammerstone percussion. *Archaeometry* 56 (6), 1085–1104.
- Blumenschine, R.J., 1986. Carcass consumption sequences and the archaeological distinction of scavenging and hunting. *J. Hum. Evol.* 15 (8), 639–659.
- Blumenschine, R.J., 1987. Characteristics of an early hominid scavenging niche. *Curr. Anthropol.* 28, 383–407.
- Blumenschine, R.J., 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *J. Archaeol. Sci.* 15, 483–502.
- Blumenschine, R.J., 1991. Hominid carnivory and foraging strategies, and the socio-economic function of early archaeological sites. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 334 (1270), 211–221.
- 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. *J. Hum. Evol.* 29 (1), 21–51.
- Blumenschine, R.J., Madrigal, T.C., 1993. Variability in long bone marrow yields of East African ungulates and its zoarchaeological implications. *J. Archaeol. Sci.* 20 (5), 555–587.
- Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. *Nature* 333 (6175), 763–765.
- Blumenschine, R.J., Selvaggio, M.M., 1991. On the marks of marrow bone processing by hammerstones and hyenas: their anatomical patterning and archaeological implications. In: *Cultural Beginnings: Approaches to Understanding Early Hominid Life-Ways in the African Savanna*, vol. 19. Habelt Verlag, Bonn, pp. 17–32.
- Blumenschine, R.J., Cavallo, J.A., Capaldo, S.D., 1994. Competition for carcasses and early hominid behavioral ecology: a case study and conceptual framework. *J. Hum. Evol.* 27 (1–3), 197–213.
- Brain, C.K., 1967. Hottentot food remains and their bearing on the interpretation of fossil bone assemblages. *Scientific papers of the Namib Desert research station* 1967 32, 1–11.
- Brain, C.K., 1969. The contribution of Namib Desert Hottentots to an understanding of australopithecine bone accumulations. *Scientific papers of the Namib Desert research station* 1969 13–22, 39.
- Bunn, H.T., 1981. Archaeological evidence for meat-eating by plio-pleistocene hominids from koobi fora and olduvai gorge. *Nature* 291 (5816), 574.
- Bunn, H.T., 1982. Meat-eating and Human Evolution: Studies on the Diet and Subsistence Patterns of Plio-Pleistocene Hominids in East Africa. Ph.D. Dissertation. University of California, Berkeley.
- Bunn, H.T., 1983. Evidence on the diet and subsistence patterns of plio-pleistocene hominids at koobi fora, Kenya, and at olduvai gorge, Tanzania. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology: Hunters and Their Prey*, vol. 163. B.A.R. International Series, pp. 21–30.
- Bunn, H.T., 1986. Patterns on skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. *J. Hum. Evol.* 15, 673–690.
- Bunn, H.T., 1991. A taphonomic perspective on the archaeology of human origins. *Annual Review of Anthropology* 20, 433–467.
- Bunn, H.T., Ezzo, J.A., 1993. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. *J. Archaeol. Sci.* 20, 365–398.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by plio-pleistocene hominids at olduvai gorge, Tanzania. *Curr. Anthropol.* 27, 431–452.
- Bunn, H.T., Kroll, E.M., 1988. A reply to Binford. *Curr. Anthropol.* 29, 123–149.
- Bunn, H.T., Pickering, T.R., 2010. Methodological recommendations for ungulate mortality analyses in paleoanthropology. *Quat. Res.* 74 (3), 388–394.
- Bunn, H.T., Gurtov, A.N., 2014. Prey mortality profiles indicate that Early Pleistocene *Homo* at Olduvai was an ambush predator. *Quat. Int.* 322, 44–53.
- Bunn, H.T., Bartram, L.E., Kroll, E.M., 1988. Variability in bone assemblage formation from Hadza hunting, scavenging, and carcass processing. *J. Anthropol. Archaeol.* 7 (4), 412–457.
- Cáceres, I., 2002. *Tafonomía de yacimientos antrópicos en karst. Complejo Galería (Sierra de Atapuerca, Burgos), Vanguard Cave (Gibraltar) y Abric Romaní (Capellades, Barcelona)*. Doctoral dissertation, Universitat Rovira i Virgili.
- Capaldo, S.D., 1995. Inferring Hominid and Carnivore Behavior from Dual-Patterned Archaeological Assemblages. Ph.D. Thesis. Rutgers University, New Brunswick.
- Capaldo, S.D., 1997. Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (Zinjanthropus), Olduvai Gorge, Tanzania. *J. Hum. Evol.* 33, 555–597.
- Capaldo, S.D., 1998a. Methods, marks, and models for inferring hominid and carnivore behavior. *J. Hum. Evol.* 35 (3), 317–320.
- Capaldo, S.D., 1998b. Simulating the formation of dualpatterned archaeofaunal assemblages with experimental control simples. *J. Archaeol. Sci.* 35, 311–330.
- Capaldo, S.D., Blumenschine, R.J., 1994. A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing in bovid long bones. *Am. Antiq.* 59, 724–748.
- Carter, D.R., Hayes, W.C., Schurman, D.J., 1976. Fatigue life of compact bone. II. Effects of microstructure and density. *J. Biomech.* 9, 211–218.
- Cavallo, J.A., Blumenschine, R.J., 1989. Tree-stored leopard kills: expanding the hominid scavenging niche. *J. Hum. Evol.* 18, 393–399.
- Cifuentes-Alcobendas, G., Domínguez-Rodrigo, M., 2019. Deep learning and taphonomy: high accuracy in the classification of cut marks made on fleshed and defleshed bones using convolutional neural networks. *Sci. Rep.* 9 (1), 1–12.
- Coard, R., Dennell, R.W., 1995. Taphonomy of some articulated skeletal remains: transport potential in an artificial environment. *J. Archaeol. Sci.* 22 (3), 441–448.
- Cobo-Sánchez, L., 2020. *Taphonomic and Spatial Study of the Archaeological Site of DS from Bed I (Olduvai Gorge, Tanzania)*. Complutense University of Madrid. PhD dissertation.
- Currey, J.D., 2006. *Bones: Structure and Mechanics*. Princeton university press.
- De Juana, S., Domínguez-Rodrigo, M., 2011. Testing analogical taphonomic signatures in bone breaking: a comparison between hammerstone-broken equid and bovid bones. *Archaeometry* 53 (5), 996–1011.
- Deino, A.L., 2012. ⁴⁰Ar/³⁹Ar dating of Bed I, Olduvai Gorge, Tanzania, and the chronology of early Pleistocene climate change. *J. Hum. Evol.* 63 (2), 251–273.
- Discamps, E., Costamagno, S., 2015. Improving mortality profile analysis in zooarchaeology: a revised zoning for ternary diagrams. *J. Archaeol. Sci.* 58, 62–76. <https://doi.org/10.1016/j.jas.2015.03.021>.
- Domínguez-Rodrigo, M., 1997a. Meat-eating by early hominids at the FLK 22Zinjanthropusite, Olduvai Gorge (Tanzania): an experimental approach using cut-mark data. *J. Hum. Evol.* 33 (6), 669–690.
- Domínguez-Rodrigo, M., 1997b. Testing meat-eating in early hominids: analysis of cut-marking processes on defleshed carcasses. *J. Hum. Evol.* 12, 169–182.
- Domínguez-Rodrigo, M., 1999. Flesh availability and bone modifications in carcasses consumed by lions: palaeoecological relevance in hominid foraging patterns. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 149 (1–4), 373–388.
- Domínguez-Rodrigo, M., 2001. A study of carnivore competition in riparian and open habitats of modern savannas and its implications for hominid behavioral modelling. *J. Hum. Evol.* 40 (2), 77–98.
- Domínguez-Rodrigo, M., Lezana, R.M., 1996. Estudio etnoarqueológico de un campamento temporal Ndorobo (Maasai) en Kulalu (Kenia). *Trab. Prehist.* 53 (2), 131–143.
- Domínguez-Rodrigo, M., Pickering, T.R., Semaw, S., Rogers, M.J., 2005. Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the function of the world's oldest stone tools. *J. Hum. Evol.* 48 (2), 109–121.
- Domínguez-Rodrigo, M., Egeland, C.P., Pickering, T.R., 2007a. Models of Passive Scavenging by Early Hominids: Problems Arising from Equifinality in Carnivore Tooth Mark Frequencies and the Extended Concept of Archaeological Palimpsests. *Breathing Life into Fossils: Taphonomic Studies in Honor of CK (“Bob”) Brain*. Stone Age Institute Press, Gosport, Indiana, pp. 255–268.
- Domínguez-Rodrigo, M., Barba, R., Egeland, C.P., 2007b. Deconstructing Olduvai: a Taphonomic Study of the Bed I Sites. Springer Science & Business Media.
- Domínguez-Rodrigo, M., Pickering, T.R., Bunn, H.T., 2010. Configurational approach to identifying the earliest hominin butchers. *Proc. Natl. Acad. Sci. USA* 107 (49), 20929–20934.
- Domínguez-Rodrigo, M., Uribelarra, D., Santonja, M., Bunn, H.T., García-Pérez, A., Pérez-González, A., Panera, J., Rubio-Jara, S., Mabulla, A., Baquedano, E., Yravedra, J., 2014b. Autochthonous anisotropy of archaeological materials by the action of water: experimental and archaeological reassessment of the orientation patterns at the Olduvai sites. *J. Archaeol. Sci.* 41, 44–68.
- Domínguez-Rodrigo, M., Yravedra, J., Organista, E., Gidna, A., Fourvel, J.B., Baquedano, E., 2015a. A new methodological approach to the taphonomic study of paleontological and archaeological faunal assemblages: a preliminary case study from Olduvai Gorge (Tanzania). *J. Archaeol. Sci.* 59, 35–53.
- Domínguez-Rodrigo, M., Pickering, T.R., Alméjida, S., Heaton, J.L., Baquedano, E., Mabulla, A., Uribelarra, D., 2015b. Earliest modern human-like hand bone from a new > 1.84-million-year-old site at Olduvai in Tanzania. *Nat. Commun.* 6 (1), 1–8.
- Domínguez-Rodrigo, M., Pickering, T.R., 2017. The meat of the matter: an evolutionary perspective on human carnivory. *Azania* 52 (1), 4–32.
- Domínguez-Rodrigo, M., Cobo-Sánchez, L., Uribelarra, D., Arriaza, M.C., Yravedra, J., Gidna, A., et al., 2017. Spatial simulation and modelling of the early Pleistocene site of DS (Bed I, Olduvai Gorge, Tanzania): a powerful tool for predicting potential archaeological information from unexcavated areas. *Boreas* 46 (4), 805–815.
- Domínguez-Rodrigo, M., Sánchez-Flores, A.J., Baquedano, E., Arriaza, M.C., Aramendi, J., Cobo-Sánchez, L., Organista, E., Barba, R., 2019. Constraining time and ecology on the zinj paleolandscapes: microwear and mesowear analyses of the archaeofaunal remains of FLK zinj and DS (bed I), compared to FLK north (bed I) and BK (bed II) at olduvai gorge (Tanzania). *Quat. Int.* 526, 4–14.
- Domínguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z., Baquedano, E., Uribelarra, D., Pérez-González, A., Gidna, A., Yravedra, J., Díez-Martín, F., Egeland, C.P., Barba, R., 2014a. On meat eating and human evolution: a taphonomic analysis of BK4b (Upper Bed II, Olduvai Gorge, Tanzania), and its bearing on hominid megafaunal consumption. *Quat. Int.* 322, 129–152.

- Domínguez-Rodrigo, M., Bunn, H.T., Yravedra, J., 2014c. 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). *Quat. Int.* 322–323, 32–43.
- Domínguez-Rodrigo, M., Cifuentes-Alcobendas, G., Jiménez-García, B., Abellán, N., Pizarro-Monzo, M., Organista, E., Baquedano, E., 2020. Artificial intelligence provides greater accuracy in the classification of modern and ancient bone surface modifications. *Sci. Rep.* 10 (1), 1–11.
- Domínguez-Rodrigo, M., Baquedano, E., Organista, E., Cobo-Sánchez, L., Mabulla, A., Maskara, V., Gidna, A., Pizarro-Monzo, M., Aramendi, J., Galán, A.B., Cifuentes-Alcobendas, G., 2021. Early Pleistocene faunivorous hominins were not kleptoparasitic, and this impacted the evolution of human anatomy and socioecology. *Sci. Rep.* 11 (1), 1–13.
- Domínguez-Rodrigo, M., Barba, R., 2007. New estimates of tooth-mark and percussion-mark frequencies at the FLK Zinj/anthropus level: the carnivore–hominid–carnivore hypothesis falsified. In: *Deconstructing Olduvai: a Taphonomic Study of the Bed I Sites*. Springer, Dordrecht, pp. 201–215.
- Domínguez-Rodrigo, M., Cobo-Sánchez, L., 2017a. A spatial analysis of stone tools and fossil bones at FLK Zinj 22 and PTK I (Bed I, Olduvai Gorge, Tanzania) and its bearing on the social organization of early humans. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 488, 21–34.
- Domínguez-Rodrigo, M., Cobo-Sánchez, L., 2017b. The spatial patterning of the social organization of modern foraging *Homo sapiens*: a methodological approach for understanding social organization in prehistoric foragers. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 488, 113–125.
- Domínguez-Rodrigo, M., García-Pérez, A., 2013. Testing the accuracy of different A-axis types for measuring the orientation of bones in the archaeological and paleontological record. *PLoS One* 8 (7), e68955.
- Domínguez-Rodrigo, M., Martínez-Navarro, B., 2012. Taphonomic analysis of the early Pleistocene (2.4 Ma) faunal assemblage from AL 894 (Hadar, Ethiopia). *J. Hum. Evol.* 62 (3), 315–327.
- Domínguez-Rodrigo, M., Organista, E., 2007. Natural background bone assemblages and their ravaging stages in Olduvai Bed I. In: *Deconstructing Olduvai: a Taphonomic Study of the Bed I Sites*. Springer, Dordrecht, pp. 201–215.
- Domínguez-Rodrigo, M., Pickering, T.R., 2003. Early hominids, hunting and scavenging: a summary of the discussion. *Evol. Anthropol.* 12, 275–282.
- Egeland, A.G., Egeland, C.P., Bunn, H.T., 2008. Taphonomic analysis of a modern spotted hyena (*Crocuta crocuta*) den from Nairobi, Kenya. *Journal of Taphonomy* 6 (3–4), 275–299.
- Faith, J.T., Gordon, A.D., 2007. Skeletal element abundances in archaeofaunal assemblages: economic utility, sample size, and assessment of carcass transport strategies. *J. Archaeol. Sci.* 34 (6), 872–882.
- 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. *J. Hum. Evol.* 56 (3), 247–256.
- 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 Jr., J.W., Hertel, F., 2013. Earliest archaeological evidence of persistent hominin carnivory. *PLoS One* 8 (4), e62174.
- Fiorillo, A.R., 1991. Taphonomy and depositional setting of Careless Creek Quarry (Judith River formation), Wheatland County, Montana, U.S.A. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 81, 281–311.
- Fisher, N.I., 1995a. *Statistical Analysis of Circular Data*. Cambridge University Press, Cambridge.
- Fisher, J.W., 1995b. Bone surface modifications in zooarchaeology. *J. Archaeol. Method Theory* 2 (1), 7–68.
- Foley, R.A., 1993. The influence of seasonality on hominid evolution. *Seasonality and human ecology* 17–37.
- Gidna, A.O., Kisui, B., Mabulla, A., Musiba, C., Domínguez-Rodrigo, M., 2014. An ecological neo-taphonomic study of carcass consumption by lions in Tarangire National Park (Tanzania) and its relevance for human evolutionary biology. *Quat. Int.* 322, 167–180.
- Grobler, J.H., 1980. Body growth and age determination of the sable *Hippotragus niger niger* (Harris, 1838). *Koedoe* 23 (1), 131–156.
- Howard, P., 2007. *Archaeological Survey and Mapping*. Taylor and Francis, London.
- Isaac, G.L., 1967. Towards the interpretation of occupation debris: some experiments and observations. *Kroeber Anthropol. Soc. Pap. (KAS J.)* 37 (37), 31–57.
- Isaac, G., 1978. The food-sharing behavior of protohuman hominids. *Sci. Am.* 238 (4), 90–109.
- Isaac, G.L., 1983. Bones in contention: competing explanations for the juxtaposition of Early Pleistocene artifacts and faunal remains. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology 1. Hunters and Their Prey*, vol. 163. B.A.R. International Series, Oxford, pp. 3–19.
- Kerbis-Peterhans, J., 1990. *The Roles of Leopards, Hyena and Porcupines in Ungulate Carcass Dispersal: Implications for Paleoanthropology* (Doctoral Dissertation, PhD Thesis). University of Chicago.
- Kiley-Worthington, M., 1965. The Waterbuck (*Kobus defassa* Ruppel 1835 and *K. ellipsiprimnus* Ogilby 1833) in East Africa: Spatial Distribution. A Study of the Sexual Behaviour.
- Klein, R.G., 1982. Age (mortality) profiles as a means of distinguishing hunted species from scavenged ones in Stone Age archaeological sites. *Paleobiology* 151–158.
- Krajcarz, M., Krajcarz, M.T., 2014. The red fox (*Vulpes vulpes*) as an accumulator of bones in cave-like environments. *Int. J. Osteoarchaeol.* 24 (4), 459–475.
- Kreutzer, L.A., 1988. Megafaunal butchering at Lubbock Lake, Texas: a taphonomic reanalysis. *Quat. Res.* 30 (2), 221–231.
- Kuhn, M., Wing, J., Weston, S., Williams, A., Keefer, C., Engelhardt, A., Cooper, T., Mayer, Z., Kenkel, B., 2020. *Caret: Classification and Regression Training. R Package Version 6.0-86*. Astrophysics Source Code Library, Cambridge, MA, USA.
- La Grange, A.M., Le Roux, N.J., Gardner-Lubbe, S., 2009. *BiplotGUI: Interactive Biplots in R*. J. Stat. Software 30, 1–37.
- Lam, Y.M., Chen, X., Pearson, O.M., 1999. Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid and equid elements in the archaeological record. *Am. Antiq.* 64, 343–362.
- Liebenberg, L., 2006. Persistence hunting by modern hunter-gatherers. *Curr. Anthropol.* 47 (6), 1017–1026.
- Linares-Matás, G.J., Clark, J., 2021. Seasonality and Oldowan behavioral variability in East Africa. *J. Hum. Evol.*, 103070.
- Loch, W.E., Bradley, M., 1998. *Determining Age of Horses by Their Teeth*. Extension publications (MU).
- Lund, U., Agostinelli, C., 2018. *CircStats: Circular Statistics*. Version 0.2-6URL.
- Lyman, R.L., 1982. Archaeofauna and subsistence studies. In: *Advances in Archaeological Method and Theory*. Academic Press, pp. 331–393.
- Lyman, R.L., 1984. Bone density and differential survivorship in fossil classes. *J. Anthropol. Archaeol.* 3, 259–299.
- Lyman, R.L., Houghton, L.E., Chambers, A.L., 1992. The effect of structural density on marmot skeletal part representation in archaeological sites. *J. Archaeol. Sci.* 19 (5), 557–573.
- Lyman, R.L., Lyman, C., 1994. *Vertebrate Taphonomy*. Cambridge University Press.
- Manilay, Z., Novitskaya, E., Sadovnikov, E., McKittrick, J., 2013. A comparative study of young and mature bovine cortical bone. *Acta Biomater.* 9 (2), 5280–5288.
- Marean, C.W., Spencer, L.M., Blumenschine, R.J., Capaldo, S., 1992. Captive hyaena bone choice and destruction, the Schlepp effect and Olduvai archaeofaunas. *J. Archaeol. Sci.* 19, 101–121.
- Marean, C.W., Spencer, L.M., 1991. Impact of carnivore ravaging of bone in archaeological assemblages. *J. Archaeol. Sci.* 18, 677–694.
- Marean, C.W., Rodrigo, M.D., Pickering, T.R., 2004. Skeletal element equifinality in zooarchaeology begins with method: the evolution and status of the "shaft critique". *Journal of Taphonomy* 2 (1), 69–98.
- Marin, J., Saladie, P., Rodríguez-Hidalgo, A., Carbonell, E., 2017. Neanderthal hunting strategies inferred from mortality profiles within the Abric Romaní sequence. *PLoS One* 12 (11), e0186970.
- Marlowe, F.W., Berbesque, J.C., 2009. Tubers as fallback foods and their impact on Hadza hunter-gatherers. *Am. J. Phys. Anthropol.: The Official Publication of the American Association of Physical Anthropologists* 140 (4), 751–758.
- Martín-Perea, D.M., Fesharaki, O., Samper, J.J.R., Arroyo, X., Uribelarra, D., Cobo-Sánchez, L., Baquedano, E., Mabulla, A., Domínguez-Rodrigo, M., 2019. Mineral assemblages and low energy sedimentary processes in the FLK-Zinj, DS, PTK and AMK complex palaeolandscape (Olduvai Gorge, Tanzania). *Quat. Int.* 526, 15–25.
- Metcalfe, D., Jones, K.T., 1988. A reconsideration of animal body-part utility indices. *Am. Antiq.* 53 (3), 486–504.
- Moclán, A., Domínguez-Rodrigo, M., Yravedra, J., 2019. Classifying agency in bone breakage: an experimental analysis of fracture planes to differentiate between hominin and carnivore dynamic and static loading using machine learning (ML) algorithms. *Archaeological and Anthropological Sciences* 11 (9), 4663–4680.
- Moclán, A., Huguet, R., Márquez, B., Laplana, C., Arsuaga, J.L., Pérez-González, A., Baquedano, E., 2020. Identifying the bone-breaker at the Navalmaillo Rock Shelter (Pinilla del Valle, Madrid) using machine learning algorithms. *Archaeological and Anthropological Sciences* 12 (2), 1–17.
- Moclán, A., Domínguez-Rodrigo, M., 2018. An experimental study of the patterned nature of anthropogenic bone breakage and its impact on bone surface modification frequencies. *J. Archaeol. Sci.* 96, 1–13.
- Munro, N.D., Bar-Oz, G., 2005. Gazelle bone fat processing in the Levantine Epipalaeolithic. *J. Archaeol. Sci.* 32 (2), 223–239.
- Murray, M.G., 1982. The rut of impala: aspects of seasonal mating under tropical conditions. *Z. Tierpsychol.* 59 (4), 319–337.
- Oelze, V.M., Head, J.S., Robbins, M.M., Richards, M., Boesch, C., 2014. Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis. *J. Hum. Evol.* 66, 95–106.
- Oliver, J.S., 1994. Estimates of hominin and carnivore involvement in the FLK Zinj/anthropus fossil assemblage: some socioecological implications. *J. Hum. Evol.* 27 (1–3), 267–294.
- Oliver, J.S., Plummer, T.W., Hertel, F., Bishop, L.C., 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. *J. Hum. Evol.* 131, 61–75.
- Organista, E., Pernas-Hernández, M., Gidna, A., Yravedra, J., Domínguez-Rodrigo, M., 2016. An experimental lion-to-hammerstone model and its relevance to understand hominin-carnivore interactions in the archaeological record. *J. Archaeol. Sci.* 66, 69–77. <https://doi.org/10.1016/j.jas.2015.12.004>.
- 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. *J. Hum. Evol.* 63 (2), 395–407.
- 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*. City University of New

- York.
- Parkinson, J.A., 2018. Revisiting the hunting-versus-scavenging debate at FLK Zinj: a GIS spatial analysis of bone surface modifications produced by hominins and carnivores in the FLK 22 assemblage, Olduvai Gorge, Tanzania. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 511, 29–51.
- Parkinson, J.A., Plummer, T.W., Oliver, J.S., Bishop, L.C., 2022. Meat on the menu: GIS spatial distribution analysis of bone surface damage indicates that Oldowan hominins at Kanjera South, Kenya had early access to carcasses. *Quat. Sci. Rev.* 277.
- Pickering, T.R., Marean, C.W., Domínguez-Rodrigo, M., 2003. Importance of limb bone shaft fragments in zooarchaeology: a response to “On in situ attrition and vertebrate body part profiles” (2002), by MC Stiner. *J. Archaeol. Sci.* 30 (11), 1469–1482.
- Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2004. New data and ideas on the foraging behaviour of Early Stone Age hominids at Swartkrans Cave, South Africa. *South Afr. J. Sci.* 100 (3–4), 215–219.
- Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2005. The contribution of limb bone fracture patterns to reconstructing early hominid behaviour at Swartkrans Cave (South Africa): archaeological application of a new analytical method. *Int. J. Osteoarchaeol.* 15 (4), 247–260.
- Pickering, T.R., Egeland, C.P., Domínguez-Rodrigo, M., Brain, C.K., Schnell, A.G., 2008. Testing the “shift in the balance of power” hypothesis at Swartkrans, South Africa: hominid cave use and subsistence behavior in the Early Pleistocene. *J. Anthropol. Archaeol.* 27 (1), 30–45. <https://doi.org/10.1016/j.jaa.2007.07.002>.
- Pickering, T.R., Egeland, C.P., 2006. Experimental patterns of hammerstone percussion damage on bones: implications for inferences of carcass processing by humans. *J. Archaeol. Sci.* 33 (4), 459–469.
- Pickering, T.R., Wallis, J., 1997. Bone modifications resulting from captive chimpanzee mastication: implications for the interpretation of Pliocene archaeological faunas. *J. Archaeol. Sci.* 24 (12), 1115–1127.
- Pizarro-Monzo, M., Organista, E., Cobo-Sánchez, L., Baquedano, E., Domínguez-Rodrigo, M., 2021. Determining the diagenetic paths of archaeofaunal assemblages and their palaeoecology through artificial intelligence: an application to Oldowan sites from Olduvai Gorge (Tanzania). *J. Quat. Sci.* vol. 37 (no 3), 543–557.
- Potts, R., 1988. *Early Hominid Activities at Olduvai*. Aldine, New York.
- R Core Team, 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Version 4.0.3.
- Reineck, H.E., Singh, I.B., 1980. Depositional environments. In: *Depositional Sedimentary Environments*. Springer, Berlin, Heidelberg, pp. 5–7.
- Ringrose, T.J., 2012. Bootstrap confidence regions for correspondence analysis. *J. Stat. Comput. Simulat.* 82 (10), 1397–1413.
- Ringrose, T., 2019. *cabootcrs: Bootstrap Confidence Regions for Simple and Multiple Correspondence Analysis*. Version 2.0.
- Rodríguez-Hidalgo, A., Saladie, P., Olle, A., Arsuaga, J.L., de Castro, J.M.B., Carbonell, E., 2017. Human predatory behavior and the social implications of communal hunting based on evidence from the TD10. 2 bison bone bed at Gran Dolina (Atapuerca, Spain). *J. Hum. Evol.* 105, 89–122.
- Rose, L., Marshall, F., 1996. Meat eating, hominid sociality, and home bases revisited. *Curr. Anthropol.* 37 (2), 307–338.
- Schaller, G.B., 1968. Hunting behaviour of the cheetah in the Serengeti National Park, Tanzania. *Afr. J. Ecol.* 6 (1), 95–100.
- Schapera, I., 1965. *The Khoisan Peoples of South Africa: Bushmen and Hottentots*. Routledge & Kegan Paul.
- Schick, K.D., 1984. *Processes of Paleolithic Site Formation: an Experimental Study*. University of California, Ph. D. dissertation, Berkeley.
- Selvaggio, M.M., 1994. *Identifying the Timing and Sequence of Hominid and Carnivore Involvement with Plio-Pleistocene Bone Assemblages from Carnivore Tooth Marks and Stone-Tool Butchery Marks on Bone Surfaces*. Ph.D. Dissertation. Rutgers University, New Brunswick.
- Speth, J.D., 1987. Early hominid subsistence strategies in seasonal habitats. *J. Archaeol. Sci.* 14 (1), 13–29.
- Speth, J.D., 1989. Early hominid hunting and scavenging: the role of meat as an energy source. *J. Hum. Evol.* 18 (4), 329–343.
- Spinage, C.A., 1967. Ageing the Uganda defassa waterbuck *Kobus defassa ugandae* Neumann. *Afr. J. Ecol.* 5 (1), 1–17.
- Spinage, C.A., 1976. Age determination of the female Grant's gazelle. *Afr. J. Ecol.* 14 (2), 121–134.
- Stein, J.K., 1987. Deposits for archaeologists. *Adv. Archaeol. Method Theor.* 11, 337–395.
- Steele, T.E., Weaver, T.D., 2002. The modified triangular graph: a refined method for comparing mortality profiles in archaeological samples. *J. Archaeol. Sci.* 29 (3), 317–322.
- Stiner, M.C., 1990. The use of mortality patterns in archaeological studies of hominid predatory adaptations. *J. Anthropol. Archaeol.* 9 (4), 305–351.
- Stiner, M.C., 1991. An interspecific perspective on the emergence of the modern human predatory niche. In: Stiner, M.C. (Ed.), *Human Predators and Prey Mortality*. Westview Press, Boulder, pp. 149–185, 1991.
- Talbot, L.M., Talbot, M.H., 1963. *The Wildebeest in Western Masailand, East Africa*. Wildl. Monogr. 3–88.
- Tomlinson, D.N.S., 1979. The feeding behaviour of waterbuck in the Lake Mcllwaine Game Enclosure. *Rhodesia Sci. News* 13 (1), 11–14.
- Tomlinson, D.N.S., 1981. Effects of the social organization of waterbuck *Kobus ellipsiprymnus ellipsiprymnus* (Ogilby 1833) on forage-habitat utilization in a Rhodesian game park. *Afr. J. Ecol.* 19 (4), 327–339. Toots 1965.
- Toots, H., 1965. Random orientation of fossils and its significance. *Rocky Mt. Geol.* 4 (2), 59–62.
- Uribelarrea, D., Domínguez-Rodrigo, M., Pérez-González, A., Vegas Salamanca, J., Baquedano, E., Mabulla, A., Musiba, C., Barboni, D., Cobo-Sánchez, L., 2014. Geoarchaeological and geometrically corrected reconstruction of the 1.84 Ma FLK zinj paleolandscape at Olduvai gorge, Tanzania. *Quat. Int.* 322–323, 7–31.
- Van Rooyen, A.F., 1993. Variation in body condition of impala and nyala in relation to social status and reproduction. *South African Journal of Wildlife Research-24-month delayed open access* 23 (2), 36–38.
- Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. *J. Hum. Evol.* 21 (1), 27–48.
- Visher, G.S., 1969. Grain size distributions and depositional processes. *J. Sediment. Res.* 39 (3).
- Voorhies, M.R., 1969. Taphonomy and population dynamics of an Early Pliocene Vertebrate Fauna, Knox County, Nebraska. In: *Contributions To Geology, Special Paper 1*. University of Wyoming.
- Winterhalder, B., 1981. Optimal foraging strategies and hunter-gatherer research in anthropology: Theory and models.
- Yezzi-Woodley, K., Terwilliger, A., Li, J., Chen, E., Tappen, M., Calder, J., Olver, P.J., 2022. Using machine learning on new feature sets extracted from 3D models of broken animal bones to classify fragments according to break agent. <https://doi.org/10.48550/arXiv.2205.10430>.
- Yravedra, J., Domínguez-Rodrigo, M., 2009. The shaft-based methodological approach to the quantification of long limb bones and its relevance to understanding hominid subsistence in the Pleistocene: application to four Palaeolithic sites. *J. Quat. Sci.*: Published for the Quaternary Research Association 24 (1), 85–96.