Tracking Early Hominin Foraging Behavior at DS Site (Bed I, Olduvai Gorge)

Frühes menschliches Ernährungsverhalten: Beiträge aus der taphonomischen und räumlichen Untersuchung von DS (Bed I, Olduvai-Schlucht)

Lucía Cobo-Sánchez

Universität zu Köln
Archäologisches Institut
Albertus-Magnus-Platz
50923 Köln, Germany
lcsanchez@ualg.pt

Institute of Evolution in Africa (I.D.E.A.)
Madrid, Spain

ABSTRACT

Academic discussions about African Early Stone Age site formation, animal carcass acquisition by hominins, the regularity of meat consumption or the use of central places have mainly relied on taphonomic studies of a few archaeofaunal assemblages, such as FLK Zinj (1.84 Ma [million years] ago, Olduvai Gorge Bed I, Tanzania). The DS site lies on the same paleosurface as FLK Zinj and constitutes an equally well-preserved, vertically-discrete deposit. The site has been extensively excavated in recent years (554 m^2) and represents an invaluable opportunity to address key and long debated issues regarding early hominin lifeways with new approaches based on using robust and reliable statistical methods, including machine learning. Taphonomic studies can also greatly benefit from including the spatial component in the interpretations of a site's formation and functionality. The results of the taphonomic and spatial study of DS point to the following behavioral components of hominin lifeways with regard to their foraging strategies: 1) regular primary access to animal carcasses; 2) selective animal carcass acquisition; and 3) collective animal carcass consumption in central-provisioning places. These features also point to cooperation and food sharing. The evidence from DS indicates that early *Homo* showed significant behavioral complexity relative to extant primates and a cohesive social structure. Two more newly discovered anthropogenically supported sites from the same period (PTK and AGS, Bed I Olduvai Gorge) that are currently being analyzed will soon shed further light on these adaptations.

Keywords: Africa, Olduvai Gorge, early Pleistocene sites, taphonomy, food provisioning, behavioral complexity

ZUSAMMENFASSUNG

Wissenschaftliche Diskussionen über die Entstehung afrikanischer Fundstellen des 'Early Stone Age', die Beschaffung tierischer Beute durch Homininen, die Regelmäßigkeit des Fleischkonsums oder die Nutzung zentraler Plätze stützen sich hauptsächlich auf taphonomische Studien einiger weniger archäofaunistischer Vergesellschaftungen, wie FLK Zinj (1,84 Ma [Millionen Jahre] alt), Olduvai-Schlucht Bed I, Tansania). Die DS-Fundstelle liegt auf der gleichen Paläooberfläche wie FLK Zinj und stellt eine ebenso gut erhaltene, vertikal eigenständige Ablagerung dar. Die Fundstelle wurde in den letzten Jahren umfangreich ausgegraben (554 m²) und bietet eine unschätzbare Gelegenheit, wichtige und lange diskutierte Fragen zur Lebensweise der frühen Homininen mit neuen Ansätzen auf der Grundlage robuster und zuverlässiger statistischer Methoden, einschließlich des maschinellen Lernens, anzugehen. Auch taphonomische Studien können von der Einbeziehung der räumlichen Komponente in die Interpretation der Entstehung und Funktionalität einer Fundstelle stark profitieren. Die Ergebnisse der taphonomischen und räumlichen Untersuchung von DS deuten auf die folgenden verhaltensmäßigen Komponenten der Lebensweise von Homininen in Bezug auf ihre Nahrungsbeschaffungsstrategien hin: 1) regelmäßiger primärer Zugang zu Tierbeute, 2) selektiver Erwerb von Tierbeute und 3) kollektiver Verzehr von Fleisch an zentralen Verpflegungsplätzen. Diese Merkmale deuten auch auf Kooperation und gemeinsame Nutzung von Nahrung hin. Die Erkenntnisse aus DS deuten darauf hin, dass der frühe *Homo* im Vergleich zu heutigen Primaten eine erhebliche Verhaltenskomplexität und eine zusammenhängende Sozialstruktur aufwies. Zwei weitere neu entdeckte, anthropogen beeinflusste Fundorte aus derselben Zeit (PTK und AGS, Bed I Olduvai-Schlucht), die sich derzeit in Analyse befinden, werden bald weiteres Licht auf diese Anpassungen werfen.

Schlagwörter: Afrika, Olduvai-Schlucht, frühe pleistozäne Fundplätze, Taphonomie, Nahrungsbeschaffung, komplexes Verhalten

Introduction

The origins of human behavior have been associated with fundamental adaptations related to subsistence and the acquisition of food resources by hominins, such as food transport to central provisioning places, food sharing and cooperation (Isaac 1978). These characteristics of human behavior may already be reflected in some East African early sites around 2 Ma (million years) ago (e.g., Isaac 1978, 1983; Bunn 1981; Domínguez-Rodrigo et al. 2007, 2021a; Bunn and Pickering 2010; Domínguez-Rodrigo and Pickering 2017). Archaeological sites where taphonomic analyses have determined a prominent anthropogenic agency in accumulation and modification are a minority in the Oldowan archaeological record (~2.6 – 1.7 Ma); however, they are essential for the reconstruction of early human behavior, and the zooarchaeological and taphonomic studies of the archaeofaunal remains at early sites play a key role in these discussions. After decades of intensive research, taphonomists have gained confidence that at least some of the African early Pleistocene assemblages were created by hominins, who transported and butchered car-

casses they obtained through primary access (Bunn 1981; Domínguez-Rodrigo et al. 2007, 2021a; Bunn and Pickering 2010; Ferraro et al. 2013; Domínguez-Rodrigo and Pickering 2017; Parkinson 2018).

However, the paucity of the archaeological record from this period has left many unanswered questions or precluded wider behavioral interpretations. Although the number of Oldowan sites has increased notably in the past decades, well-preserved, vertically discrete, extensively exca-vated hominin-made assemblages from around 2 Ma ago are scarce. Until recently, only FLK Zinj from Bed I in Olduvai Gorge (Tanzania) fit this description (Bunn and Kroll 1986; Domín-guez-Rodrigo et al. 2007). Other well-known and prolific regions preserving early assemblages that have provided data for numerous studies, like the ones recovered at Kanjera South or at Koobi Fora (Kenya), dated to 2.0 - 1.6 Ma, have also been interpreted as the result of hominins having primary access to the accumulated and butchered carcasses (Bunn et al. 1980; Plummer et al. 2009; Plummer and Bishop 2016; Oliver et al. 2019; Parkinson et al. 2022). Kanjera South, however, is a time-averaged deposit that could represent multiple depositional processes and agencies (Ferraro et al. 2013). Recent analyses of three archaeofaunal assemblages from Okote Member at Koobi Fora, FwJj14A, FwJj14B, and GaJi14 (~1.5 Ma) also show that *H. erectus* had access to well-fleshed carcasses (Pobiner et al. 2008), although, surprisingly, stone tools have not been found in association with faunal remains at these sites.

The recent discovery of DS (David's Site, 1.84 Ma) in Olduvai Gorge and two additional an-thropogenic accumulations on the same paleosurface as FLK Zinj (PTK and AGS) that are well-preserved, vertically-discrete and extensive deposits, with clear functional association between stone tools and faunal remains, represents a new and invaluable opportunity to address key and long debated issues regarding early hominin lifestyles: the identification of the main agents of site formation, the hunting or scavenging behavior of hominins, the socioeconomic function of sites, and the behavioral complexity of hominins relative to extant primates.

Apart from the availability of high-integrity and high-resolution archaeological data, the pos-sibility of addressing these issues also rests upon the articulation and structuring of hypotheses about human behavior. Since behavioral features are often functionally interrelated and depend-ent on each other, they can be contemplated within a systemic view of human behavior (Brooks et al. 1991). This also means that hypotheses about human behavior would also be intercon-nected. The support of one particular hypothesis thus enhances the heuristic value of the asso-ciated hypotheses (Popper 1972; Niiniluoto 1987; Bunge 1998; Domínguez-Rodrigo 2012). This view of behavior increases the amount of knowledge that can be empirically contrasted and helps us ask wider questions about the evolution of human behavior. For example, increased meat-eating is expected to have had physical, cognitive and socioecological consequences and affected broader patterns of adaptation (Isaac 1978, 1983; Bunn 1981; Fowley 1996; Domín-guez-Rodrigo et al. 2007). Moreover, meat-eating is not independent from the fact that it oc-curred on specific locations where materials accumulated in very high densities, and food sharing requires food to be brought back to a protective spot to be distributed. The intertwined hypotheses contrasted here are framed on the theory that 'human behavior emerged when sub-

sistence was based on a cooperative and solidarious social organization' (Domínguez-Rodrigo 2012).

In this paper we therefore aim to answer the following questions based on the available taphonomic evidence from DS: Were hominins having regular primary access to animal carcasses? Were hominins selectively hunting small and medium-sized ungulates? Did collective animal carcass consumption take place in central-provisioning places? And did hominins already engage in cooperative and food sharing behaviors?

Today, after a period of considerable development including experimental and actualistic work, archaeological taphonomy counts with a substantial number of approaches and methods that allow the scientific contrasting of hypotheses and assumptions (Lyman 1994; Domínguez-Rodrigo et al. 2011, 2014). This does not mean, however, that each of the taphonomic aspects usually explored in archaeofaunal studies (site formation, skeletal part profiles, bone breakage patterns, bone surface modifications and prey mortality profiles) do not have limitations. In fact, taphonomic methods still face a number of challenges, mainly dealing with small sample sizes, subjectivity when interpreting certain bone surface marks or lack of frames of reference that lead to scenarios of equifinality. Some of these limitations can be mitigated through the use of more robust statistical methods including the combination of variables designed to overcome equifinality and the use of computer vision to identify bone surface modifications (e.g., Domínguez-Rodrigo and Yravedra 2009; Domínguez-Rodrigo and Baquedano 2018; Domínguez-Rodrigo 2019; Jiménez-García et al. 2020).

By means of several examples of the analyses included in the taphonomic study of DS (Cobo-Sánchez 2020) that contain the most relevant evidence regarding hominin foraging behavior, we intend to shed light on the questions outlined above. The complete taphonomic study of DS, however, includes an analysis of site integrity, comprising the examination of bone orientation patterns, specimen size distribution and bone shape and composition. This analysis is used to test the hypotheses that the site is autochthonous, that the distortion of the assemblage through water currents can be excluded, and thereby that the spatial properties of the assemblage have remained intact (Domínguez-Rodrigo et al. 2019a). Skeletal part abundances were analyzed with relation to food utility and return rates. Long limb bone representation was compared to meaty long bone element ratios at other Paleolithic sites in an effort to address site functionality and hominin carcass transport strategies. Bone breakage patterns were approached on the one hand following traditional methods, including a number of indices, ratios, comparison of means and confidence intervals of breakage planes, as well as correspondence analyses of notch type distributions, and on the other hand using machine learning analyses combining several variables (Moclán et al. 2019). Similarly, bone surface modification analyses also included several different approaches that ranged from univariate comparisons of cut mark, percussion mark and tooth mark frequencies with experimental data and with data from other sites to machine learning analyses combining several variables. The same datasets were used in the different approaches in order to show how the latter really contribute to eliminate equifinality in every analysis.

Most of the available experimental data modeling different types of access to carcasses by hominins and carnivores was incorporated. Additionally, the anatomical location of cut marks was analyzed in addition to their frequencies. The taphotype approach, which is very useful to classify assemblages as hominin- or carnivore-made according to the predominant patterns of long bone portion deletion and modification (Domínguez-Rodrigo et al. 2015b), has also been applied. Finally, bovid mortality profiles were analyzed using multivariate statistics in addition to triangular graphs, hoping to overcome the limitations of equifinality sometimes yielded by the latter, and to gain more insight into the differences between carnivores and humans in prey distribution by age.

The taphonomic study of the archaeofauna at DS also included comparisons with other Paleolithic sites, especially with other Bed I sites, but also with sites from more recent periods and other geographical locations where anthropogenic accumulations were purportedly created by hominins having primary access to carcasses mainly through hunting. In all of the presented analyses the data from FLK Zinj was included in combination with data from DS with the intention to find similarities and differences between both pene-contemporaneous sites, and to try to assess hominin behavioral variability during Olduvai Bed I times.

The following section introduces the DS site and the next sections outline how the three main analyses and results support each of the afore-mentioned hypotheses, and draws an overall picture of hominin lifeways 1.84 Ma ago in Olduvai Gorge.

The DS Site

Olduvai Gorge is located in northern Tanzania, southeast of the Serengeti Plains (Fig. 1A). The oldest sediments it contains are around 2 Ma old. Over the past 200 ka (thousand years) fluvial erosion has carved through the different geological layers creating the gorge, which splits into two branches, the main and the secondary gorge. Hay (1976) defined several geological units within the gorge that are still the foundation for geological studies at Olduvai today: Beds I, II, III, IV, the Masek, Ndutu and Naisiusiu Beds. DS lies in Bed I, which spans from approximately 1.98 Ma to 1.75 Ma, and is formed by the alternating deposition of clayey facies associated to lake sediments and silty layers on the one hand and volcanic tuffs (1A – 1F) that have been securely dated on the other hand (Walter et al. 1991, 1992; Manega 1993; Blumenschine et al. 2016).

Several important sites are known from the layers occurring between these tuffs, like FLKN, FLKNN and DK, but the four fully anthropogenic sites discovered in Bed I (FLK Zinj, PTK, DS, and AGS) all stem from the paleosol underlying Tuff 1C, which contains a clay stratum (<20 cm; Levels 22A and 22B) that can be traced laterally on a significant portion of the gorge at the junction and on both ends of its trajectory in areas that lay close to an ancient lake (Fig. 1B, 1C; Fig. 2).

DS (1.84 Ma) is located at the junction between the main and secondary branches of Olduvai Gorge in northern Tanzania (2º59'33"S; 35º21'08"E). It was discovered a few hundred meters away from FLK Zinj, in an area covered by a dirt road. Excavations started immediately after its
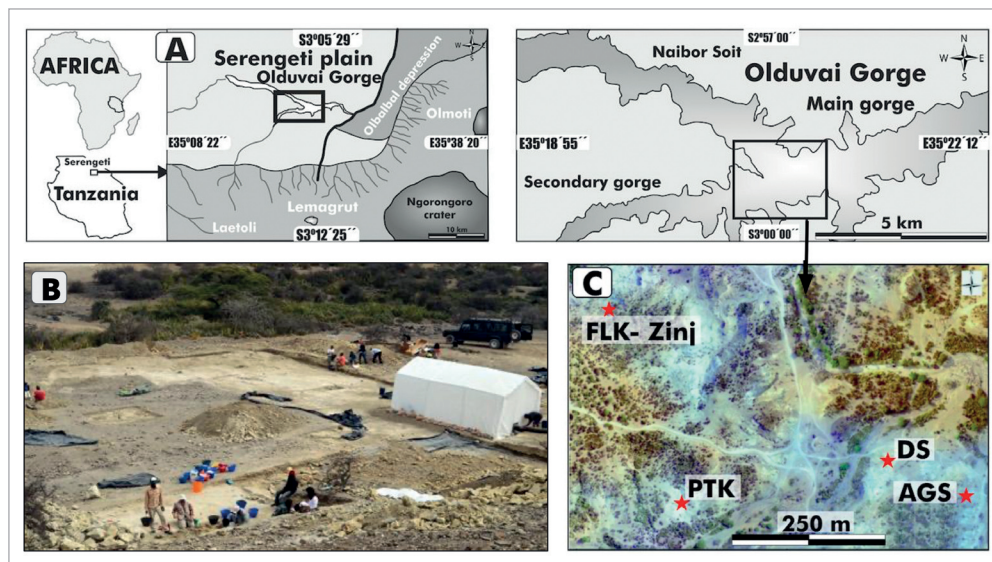
Fig. 1: A) Location of Olduvai Gorge and the Zinj paleolandscape in northern Tanzania; B) General view of the DS excavation in 2015 from the south; C) Location of FLK Zinj, DS, PTK and AGS in the junction between the main and secondary branches of Olduvai Gorge (modified from Diez-Martín et al. 2021).

Abb. 1: A) Lage der Olduvai-Schlucht und der Zinj-Paläolandschaft im Norden Tansanias; B) Gesamtansicht der DS-Grabung im Jahre 2015 von Süden; C) Lage von FLK Zinj, DS, PTK und AGS an der Kreuzung zwischen dem Haupt- und Nebenarm der Olduvai-Schlucht (modifiziert nach Diez-Martín et al. 2021).

discovery revealing dense clusters of fossils and stone tools in situ, and went on for five field seasons (Fig. 1B). From 2014 to 2018, intensive excavations exposed an area of 554 m². DS is therefore larger than the pene-contemporaneous FLK Zinj and FLK NN 1 sites and constitutes the biggest open window to the African Early Pleistocene to date. Over the course of these five fieldwork seasons, more than 15,000 fossil remains and stone tools (including sieve finds) were recovered from Level 22B. Level 22A contained archaeological remains as well, yet in much lower densities. Excavations proceeded quickly during the first two field seasons, because the archaeological deposit was found at just a few centimeters below the surface. Excavations of DS were initially conducted on the basalt platform and at the outcrop on both sides of the road. The arc-shaped excavation is caused by an erosive gap in between both areas.

DS stands out not only for the density of materials, but also for their spatial extension. By the end of the 2015 field season, excavations had already exposed a large area. At this point, a spatial statistical prediction using different regression models and simulations was carried out in order to detect the potentially densest portions of the unexcavated areas of DS (Domínguez-Rodrigo et al. 2017). The high correspondence between the results obtained from these predictions and subsequent excavations at the site showed the great potential of the application of spatial statistical techniques in archaeological research.
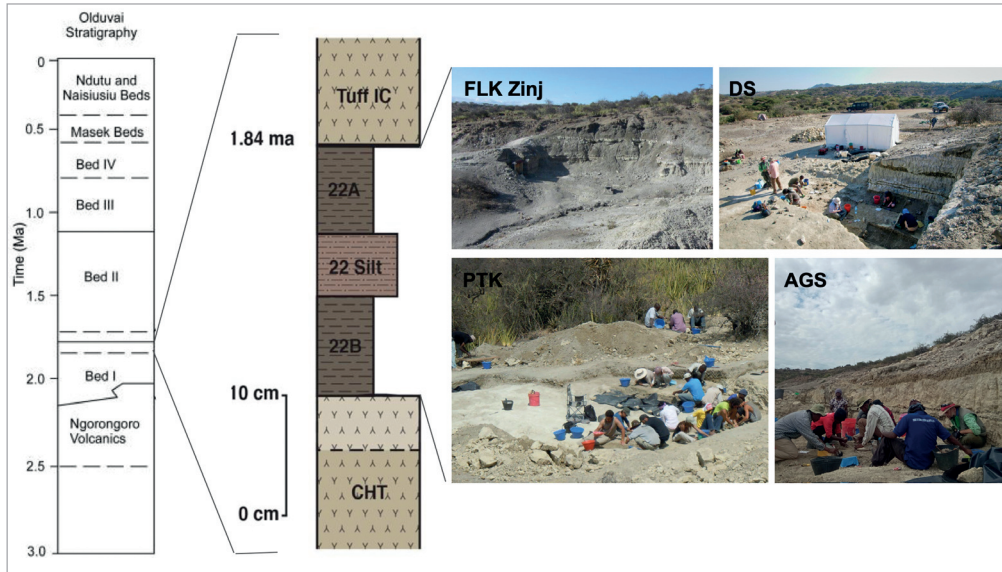
Fig. 2: Chronostratigraphic position of the sites mentioned in the text.
Abb. 2: Chronostratigraphische Stellung der im Text erwähnten Fundstellen.

At the end of the 2016 field season, most of the paleosurface (468 m²) had been exposed and abundant fossil bones and lithic remains had been retrieved from both archaeological levels. In addition, a series of sediment samples were taken from some of the trenches for chemical bio-marker analyses. The trenches excavated in 2017 towards the south of the site area yielded somewhat lower fossil densities than those excavated in previous field seasons, suggesting that the limits of the site towards that direction could be close. The trend observed for level 22A was the opposite, however.

In 2018, several additional trenches were opened with the intention of demarcating the site boundaries. Indeed, these excavated trenches yielded lower densities of archaeological materials, establishing site limits and excavations were finalized. It was determined that some of the edges of the site were delimited by erosion. This was especially true of the central area where deposition and erosion of the Ndutu unconformable sediments exposed the underlying clay to modern erosion. In addition, the southern edge of the excavation began yielding lower densities of materials due to a change in facies from clayey to silty sediments, which probably indicated a change in the paleolandscape. The remaining areas are limited by the lava flows of the bottom of Bed I that were already part of the paleolandscape when hominins created the site (Uribelarrea et al. 2014) (Fig. 3a).

Preservation of the fossil bones at DS is comparable to that at FLK Zinj. This suggests that post-depositional processes had a marginal effect on the assemblage. The numerous rib and vertebrae remains recovered support this inference, because these usually disappear due to the ac-
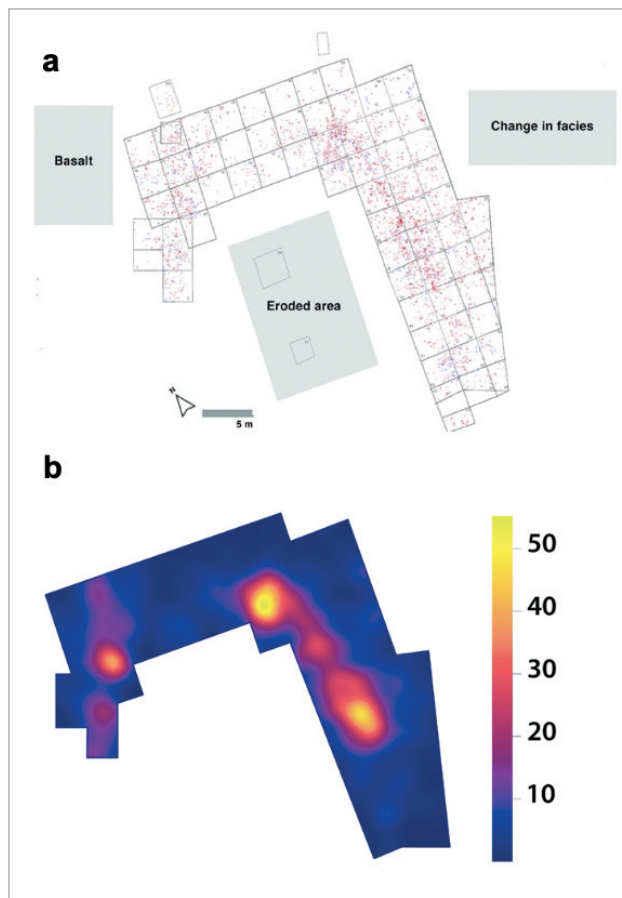
Fig. 3: a) Site plan of the excavation of level 22B at DS showing the distribution of the recovered archaeological materials >20 mm. The site is delimited by erosion, ancient lava flows and a change in facies. In the central area of the site, the deposition of the Ndutu unconformable sediments and their subsequent erosion had exposed the clay deposit to the effect of rains and the use of the area as a road; b) Kernel density map of the archaeofaunal remains recovered in Level 22B. Scale refers to archaeological remains (bones and lithics) per square meter (modified from Cobo-Sánchez 2020).

Abb. 3: a) Lageplan der Ausgrabung des Niveaus 22B der Fundstelle DS, der die Verteilung der geborgenen archäologischen Materialien >20 mm zeigt. Die Stelle ist durch Erosion, alte Lavaströme und eine Veränderung der Fazies begrenzt. Im zentralen Bereich des Geländes hatten die Ablagerung der diskordanten Ndutu-Sedimente und ihre anschließende Erosion durch Regen und die Nutzung des Gebiets als Straße die Tonablagerung freigelegt; b) Kerndichtekarte der archäofaunistischen Überreste, die in Niveau 22B geborgen wurden. Der Maßstab bezieht sich auf archäologische Überreste (Knochen und Steinartefakte) pro Quadratmeter (modifiziert nach Cobo-Sánchez 2020).

tion of carnivores or hydraulic processes (Domínguez-Rodrigo et al. 2018). The site seems to have formed in a short period of time, less than two or three years (Domínguez-Rodrigo et al. 2019b), and the ecological conditions at the site can be reconstructed with very high resolution. Thus, many taphonomic, behavioral, and ecological relationships can be explored spatially.

Level 22B from DS contains around 85% of the faunal remains recovered from the site. This level has yielded 3458 bone fragments and 1182 lithics (if counting the fraction longer than 20 mm). The average fossil density in this archaeological level is about eight pieces per square meter, but archaeological materials cluster around three areas of very high fossil density (around 70 remains per square meter) (Fig. 3b). The opposite occurs at PTK, FLK Zinj and AGS where the bulk of the archaeofaunal assemblage and the associated lithic tools come from the uppermost section of the Zinj clay (i.e., 22A) (Leakey 1971; Stancampiano et al. 2022; Organista et al. in press). The zooarchaeological and taphonomic analysis summarized here focused on the ungulate remains from Level 22B at DS. The taphonomic study focused almost exclusively on the

ungulate remains, because they represent the bulk of the bone assemblage (98.8%) and also reflect hominin activity most directly, which was the primary aim of the study. A comprehensive analysis of the remaining faunal sample, which mainly includes birds and small carnivores, could provide relevant information about the ecological conditions at the site. Level 22A has also provided evidence of hominin activity at the site yet, it seems, not as conspicuous as Level 22B.

Regular primary access to animal carcasses

Addressing whether hominins had early and primary access to carcasses is necessary to justify food surplus and intentional food sharing. If abundant meat and butchery and primary access to carcasses is confirmed then active foraging strategies, food transport, food sharing and cooperation are more likely, since primary access is a prerequisite for these behaviors.

Primary access to carcasses at DS would be supported by high frequencies of cut marked and percussion marked bone specimens that coincide with the corresponding experimental scenarios (e.g., Domínguez-Rodrigo 1997; Domínguez-Rodrigo and Barba 2005; Galán et al. 2009), by the location of cut marks on hot zones in long bones evidencing filleting (Domínguez-Rodrigo et al. 2007), and on ribs and/or vertebrae evidencing evisceration (Binford 1981; Bunn 1982). We would also expect a high proportion of dynamic long bone breakage (including a high number of impact flakes and type A notches) (e.g., Moclán and Domínguez-Rodrigo 2018), and lack of typical felid damage patterns on the bones (including taphotypes typically associated with felids). In addition, we should find taxonomic diversity that would contrast with a highly specialized felid predatory range (Domínguez-Rodrigo 2012).

Systematic evidence of exclusive hominin flesh exploitation and evidence of the complete butchering process of several carcasses, from evisceration to the access to the marrow content of bones, supports that meat was consumed abundantly at DS. Moreover, the accumulation on the same spot of several animals spanning carcass sizes from 1 to 3-4 (following Brain 1981), especially of animals that weigh >100 kg, that show evidence of having been defleshed entirely or primarily by hominins, suggests that meat was sufficiently abundant to be shared collectively. Both small and medium-sized carcasses present high frequencies of cut marked and percussion marked bones that coincide with hominin-to-carnivore scenarios. As an example, Figure 4 and Tables 1 and 2 show the results of the classifications of the DS and FLK Zinj bone surface mark samples using a multiple discriminant analysis with a canonical variate approach on a bootstrapped sample of the experimental assemblages of the Hominin-Carnivore (dark blue alpha bag), Felid-Hominin (dark green alpha bag), Felid-Hominin-Hyenid (light green alpha bag) models. Table 3 shows the classification results of several statistical machine learning algorithms into primary or secondary access of DS. All methods yield 100% accuracy. Classifications were nearly always higher than 95% and overall, DS is classified as primary access more than 80% of the times. Moreover, cut mark percentages coincide with those documented at several Upper Paleolithic sites as well as those reported for FLK Zinj (Cobo-Sánchez 2020). Cut marks have been found on all skeletal parts, including ribs (indicating that animals were eviscerated by

Table 1: Cut mark, percussion mark and tooth mark frequencies in the corrected sample from DS 22B as used in the statistical analyses. The correction for dry broken bones is calculated by using the sample with good cortical preservation, dividing the dry-broken bone sample by two and adding this value to the green-broken bone sample.

Tabelle 1: Schnittmarken-, Schlagmarken- und Zahnmarkenfrequenzen in der korrigierten Probe aus DS 22B, wie in den statistischen Analysen verwendet. Die Korrektur für trocken gebrochene Knochen wird berechnet, indem die Probe mit guter kortikaler Erhaltung verwendet wird, die Probe des trocken gebrochenen Knochens durch zwei dividiert und dieser Wert zu der Probe des grün gebrochenen Knochens addiert wird.

	Small carcasses (size 1-2)	Medium-sized carcasses (size 3-4)
Cut marks	11.7%	25.0%
Percussion marks	7.4%	20.1%
Tooth marks	5.6%	3.7%

Table 2: Predictions of the multiple discriminant analysis model. Classifications of DS samples in the three experimental models. The well-preserved and corrected DS sample (DSa) is classified as primary access with a probability of 99%, DSb, which includes moderately preserved cortical surfaces, is classified as primary access with a probability of 96%, and the uncorrected sample is classified with the Felid-Hominin experiments with a probability of 34%. H-C = Hominin-Carnivore; F-H = Felid-Hominin; F-H-H = Felid-Hominin-Hyenid.

Tabelle 2: Vorhersagen des multiplen Diskriminanzanalysemodells. Klassifikationen von DS-Proben in den drei experimentellen Modellen. Die gut erhaltene und korrigierte DS-Probe (DSa) wird mit einer Wahrscheinlichkeit von 99 % als primärer Zugang klassifiziert, DSb, die mäßig erhaltene kortikale Oberflächen enthält, wird mit einer Wahrscheinlichkeit von 96 % als primärer Zugang klassifiziert, und die unkorrigierte Probe wird bei den Felide-Hominine-Experimenten mit einer Wahrscheinlichkeit von 34% klassifiziert. H-C = Hominine-Carnivore; F-H = Felide-Hominine; F-H-H = Felide-Hominine-Hyäne.

	H-C	F-H	F-H-H
DSa	0.999	0.000	0.001
DSb	0.957	0.000	0.028
DSc	0.001	0.000	0.340

hominins), vertebrae and skulls. Additionally, most cut marks appear on midshafts of meaty long bones, which suggests not much disarticulation was carried out (Fig. 5a). In fact, the systematic presence of cut marks on hot zones reveals that hominins were accessing fleshed carcasses (Fig. 5b). Lower cut mark percentages are documented on LLB than on ULB and ILB. Several fragments present both cut marks and percussion marks. Only 5% of the long bone MNE were complete, and fragmentation ratios are high, suggesting that marrow was intensively exploited. Most bone breakage is also attributed to hominins by machine learning algorithms (Cobo-Sánchez 2020).

With regard to carnivore damage specifically, the low tooth mark percentages documented on different portions of the bones, also mostly coincide with hominin-to-carnivore models. The presence of felid modification patterns on the carcasses would be indicative of scavenging. Typi-
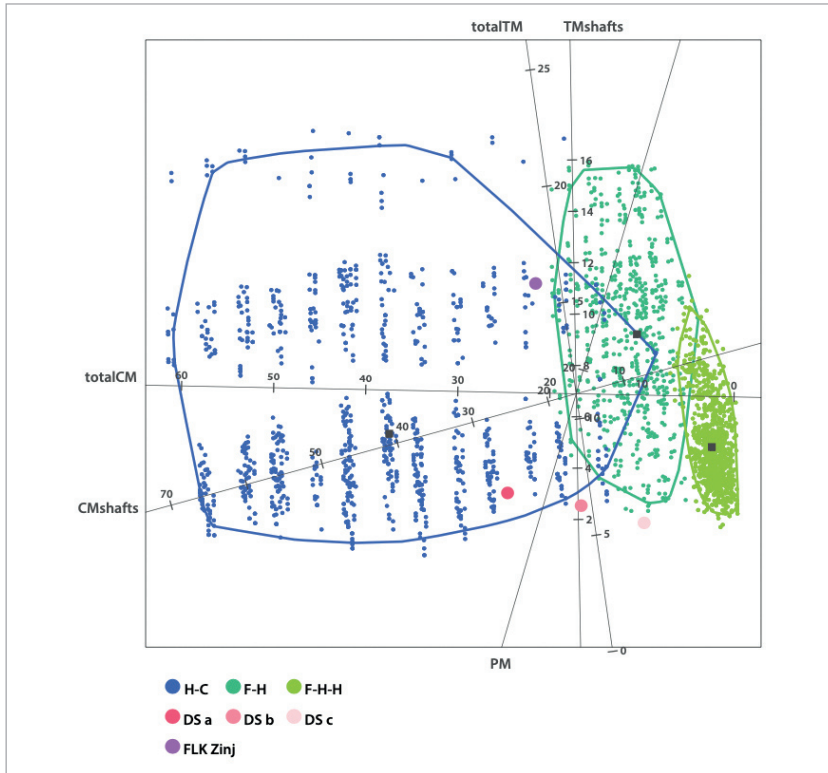
Fig. 4: Multiple discriminant analysis using a canonical variate approach on a bootstrapped sample of the experimental assemblages of the Hominin-Carnivore (dark blue alpha bag), Felid-Hominin (dark green alpha bag), Felid-Hominin-Hyenid (light green alpha bag) models. The MDA correctly classified 91.9% of the experimental sample. The experimental sample included is described in Domínguez-Rodrigo et al. (2014) and Cobo-Sánchez (2020). Cut mark frequencies were more discriminatory than percussion marks and tooth marks. The well-preserved DS assemblage appears within the 95% confidence alpha distribution of the Hominin-Carnivore model and is placed, as is the case for FLK Zinj, towards the right elongation of the Hominin-Carnivore alpha distribution, which includes experiments reproducing bulk flesh removal. DSa refers to the subsample corrected for poor and moderate preservation as well as dry breakage; DSb refers to the sample with moderately preserved bones; DSc refers to the complete uncorrected sample (modified from Cobo-Sánchez 2020).

Abb. 4: Die Multiple Diskriminanzanalyse verwendet kanonische Zufallsvariablen mithilfe der Bootstrapping-Stichprobeauswahl aus Modellen experimenteller Inventare modifiziert durch Hominine-Carnivore [Fleischfresser] (dunkelblauer Alpha-Verteilung), Felide-Hominine (dunkelgrüner Alpha-Verteilung), Felide-Hominine-Hyäne (hellgrüner Alpha-Verteilung) Modelle. Der MDA klassifizierte 91,9 % der Versuchsprobe korrekt. Die hier enthaltene experimentelle Probe ist in Domínguez-Rodrigo et al. (2014) und Cobo-Sánchez (2020) beschrieben. Schnittmarkenhäufigkeiten waren diskriminierender als Schlagmarken und Zahnmarken. Das gut erhaltene DS-Inventar erscheint innerhalb der 95%-Konfidenz-Alpha-Verteilung des Hominine-Carnivore-Modells und wird, wie im Fall von FLK Zinj, in Richtung der rechten Verlängerung der Hominine-Carnivore-Alpha-Verteilung platziert, welche Experimente beinhaltet, die die Entfernung von Fleischmengen reproduzieren. DSa bezieht sich auf die korrigierte Stichprobe ohne Knochen mit schlechter und mäßiger Erhaltung sowie mit trockenen Brüchen; DSb bezieht sich auf die Stichprobe mit mäßig erhaltene Knochen; DSc bezieht sich auf die vollständige unkorrigierte Stichprobe (modifiziert nach Cobo-Sánchez 2020).

Table 3: Accuracy percentages of correct classification of the used ML statistical algorithms and classification into primary or secondary access of DS. The sample used is the same as in the previous multivariate analysis. All methods yield 100% accuracy. Classifications were nearly always higher than 95%. Overall, DS is classified as primary access more than 80% of the cases.

Tabelle 3: Genauigkeitsprozentsätze der korrekten Klassifizierung der verwendeten ML-Statistikalgorithmen und Klassifizierung in primären oder sekundären Zugriff in DS. Die verwendete Stichprobe ist die gleiche wie in der vorherigen multivariaten Analyse. Alle Methoden liefern 100% Genauigkeit. Die Klassifizierungen waren fast immer höher als 95%. Insgesamt wird DS in mehr als 80% der Fälle als primärer Zugriff eingestuft.

Method	Accuracy	DSa	DSb	DSc
Support Vector Machine (SVM)	100	primary (NA)	primary (NA)	primary (NA)
K Nearest Neighbor (KNN)	100	secondary (1)	secondary (1)	primary (1)
Random Forest (RF)	100	primary (0.684)	primary (0.580)	secondary (0.730)
Mixture Discriminant Analysis (MXDA)	100	primary (1)	primary (1)	primary (1)
Naive Bayes	100	primary (1)	primary (1)	secondary (0.99)
Partial Least Square (PLS)	100	primary (0.995)	primary (0.981)	primary (0.999)
Neural Net (NN)	100	primary (0.997)	primary (0.996)	primary (0.997)

cal modification patterns in felid-consumed carcasses include deep pits on the mesio-lateral sides of the distal femoral troclea, damage on the caudal medial epicondyle of humeri, furrowing of the olecranon of the ulna, on the tibial crest, the pelvic crest, the scapula blade and on the vertebral apophyses, and pits or punctures on vertebral bodies (Gidna et al. 2015; Domínguez-Rodrigo et al. 2021b). DS lacks these types of modifications. The lack of typical felid damage on bones (taphotypes) associated to felids indicate that hominins were not confronting felids for their prey. Only one specimen shows modifications attributable to a felid, as well as cut marks (Domínguez-Rodrigo et al. 2021a). The remaining tooth marks on DS bone surfaces have all been attributed to hyenas by computer vision through deep learning methods (Cobo-Sánchez et al. 2022). In sum, univariate, multivariate and machine learning analyses of bone surface modifications yield consistent and uniform results pointing overwhelmingly to primary access to carcasses by hominins.

Selective animal carcass acquisition

Bovid representation at DS is very similar to that in FLK Zinj. With some exceptions, almost the same taxa are represented at both sites in similar proportions (Table 4). This shows that hominins focused on a range of carcass sizes from 1 to 3-4 and probably targeted certain species and age classes. There are almost 30 bovids represented at DS that reach size 3-4 in their adult stage, as well as five small (size 1-2) bovids and at least five large (size 5) animals. Skeletal part profiles are relatively unbiased, especially those of small carcasses. Small carcass transport seems to have followed an unconstrained strategy; they entered the site complete and were entirely processed. This might be suggestive of short-distance transport from the kill site. In medium-
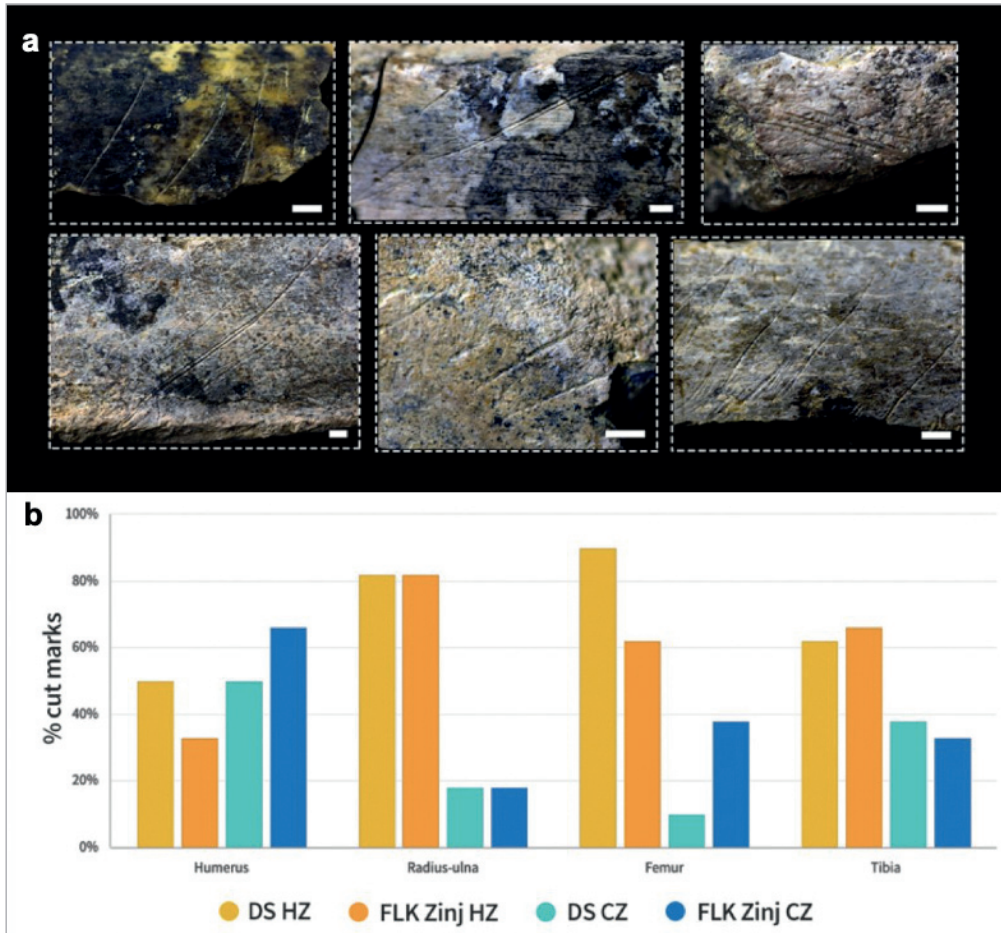
Fig. 5: a) Several examples of cut-marked long bone shafts (modified from Cobo-Sánchez 2020); b) Bar chart showing the distribution of cut marks on hot zones and cold zones on long bones in medium-sized carcasses at DS (N=49) and FLK Zinj (N=58). When lions have consumed their prey, hot zones (HZ) on long bones indicate areas where there are no flesh scraps left opposed to cold zones (CZ) where flesh scraps are present. At DS and FLK Zinj, cut marks are predominantly found on hot zones.

Abb. 5: a) Mehrere Beispiele für Langknochenschäfte mit Schnittspuren (modifiziert nach Cobo-Sánchez 2020); b) Balkendiagramm, das die Verteilung von Schnittspuren in ‚heißen' Zonen und ‚kalten' Zonen an Langknochen in mittelgroßen Karkassen bei DS (N=49) und FLK Zinj (N=58) zeigt. Wenn Löwen ihre Beute verzehrt haben, zeigen ‚heiße' Zonen (HZ) auf Langknochen Bereiche an, in denen keine Fleischreste mehr vorhanden sind, im Gegensatz zu ‚kalten' Zonen (CZ), in denen Fleischreste vorhanden sind. Bei DS und FLK Zinj finden sich Schnittmarken überwiegend in ‚heißen' Zonen.

sized carcasses, the appendicular skeleton presents a bias that is not explained in terms of food utility or density-mediated attrition, but seems to reflect particular transport decisions, as explained below (Fig. 6; Cobo-Sánchez 2020).

Regular primary access to carcasses as evidenced at DS is necessarily linked to hunting as the main foraging strategy used by hominins to accumulate carcasses at DS. Hunting would be supported by bovid age profiles that differ from the preys of carnivores and/or show similarities to prime adult-dominated profiles typical in many sites of more recent periods of human evolution and age profiles generated by modern hunter-gatherers (e.g. Bunn and Pickering 2010). Hunting would also be supported if the taphotypes did not match those created by felids. It could also be supported potentially by impact marks from sharp or pointed objects on the bones (Gaudzinski-Windheuser et al. 2018). Indeed, several taphonomic results support this foraging strategy. As explained above, taphotypes at DS do not coincide with those typical for felids. Most

Table 4: Minimum number of bovids represented (MNI) by cranial/mandibular elements at FLK Zinj (Domínguez-Rodrigo et al. 2007) and DS 22B (modified from Cobo-Sánchez 2020).

Tabelle 4: Mindestzahl der durch Schädel-/Unterkieferelemente repräsentierten Boviden (MNI) bei FLK Zinj (Domínguez-Rodrigo et al. 2007) und DS 22B (modifiziert nach Cobo-Sánchez 2020).

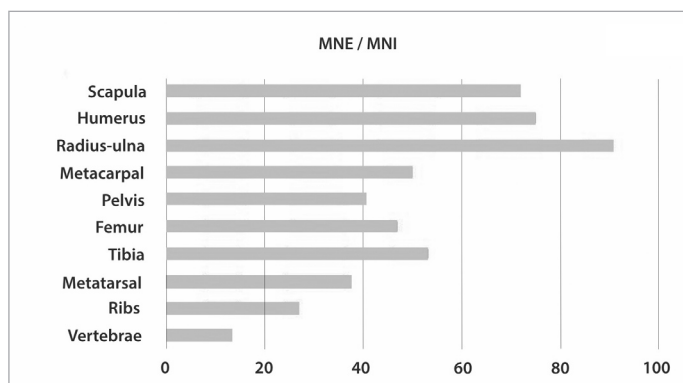| Taxon	FLK Zinj	DS
Antidorcas recki	7	5
Parmularius altidens	4	4
Connochaetes sp.	2	4
Kobus sigmoidalis	7	11
Tragelaphus strepsiceros	0	1
Megalotragus sp.	0	2

Fig. 6: Skeletal part profiles for medium-sized bovids (size 3-4) from DS 22B that result from calculating the proportion of MNE represented per MNI.

Abb. 6: Skelettteilprofile für mittelgroße Boviden (Größe 3-4) aus DS 22B, die sich aus der Berechnung des MNE-Anteils pro MNI ergeben.

overlap in the documented mortality profiles of medium-sized bovid carcasses from DS with other assemblages occurs with the Hadza/Kua kills when using the triangle graphs (Fig. 7). Apart from the fact that bovid age profiles at DS do not coincide with age profiles usually created by other carnivores, the bovid accumulations at DS (and FLK Zinj) are both dominated by prime adults (60-70%), something common in many other archaeological sites that are anthropogenic, and which is consistent with ambush hunting (Table 5; Fig. 7).

Large amounts of meat could only have been available regularly for hominins if they acquired carcasses either through hunting and/or through confrontational scavenging, because in savanna biomes only marginal carcass resources are available for scavenging, and only for short periods of time during the end of the dry season (e.g., Blumenschine 1986). Regular confrontational scavenging could therefore also yield relatively fleshed carcasses. However, this foraging strategy should be supported by age profiles similar to the prey targeted by felids, a predominance of typical felid modification patterns (Domínguez-Rodrigo et al. 2015b), and an anatomical distribution and frequency of cut marks and tooth marks that correspond with a felid to hominin to hyenid scenario, none of which characterize the DS archaeofaunal assemblage. As explained above, there is only one documented case of felid damage in the complete assemblage that suggests confrontational scavenging (Domínguez-Rodrigo et al. 2021b). There is, however, a bias in the representation of front and hind limbs consisting in a lower representation of the highest utility parts (hind limbs) that could indicate that some medium-sized carcasses where acquired
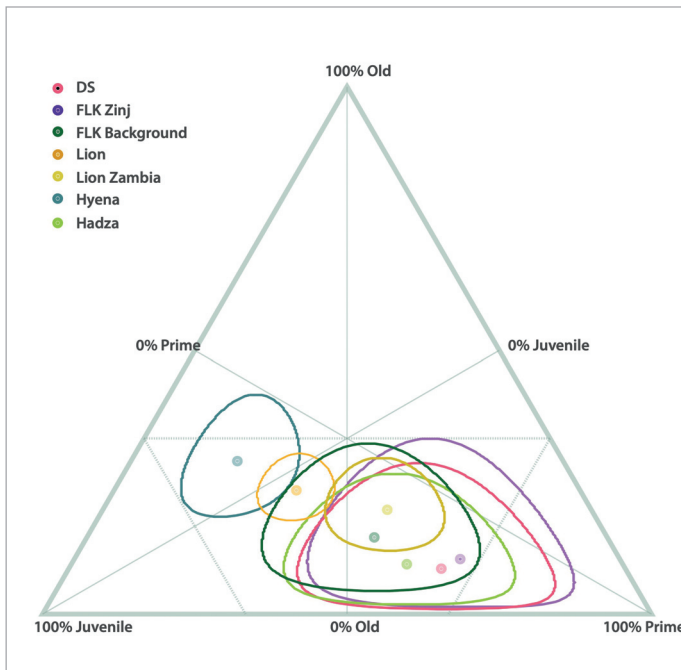

Fig. 7: Triangle graph showing the mortality patterns for medium-sized bovids killed by lions, hyenas, cheetahs, leopards, wild dogs, and Hadza and Kua hunter-gatherers (using data from Bunn and Pickering 2010 and Bunn und Gurtov 2014), as well as the mortality profiles documented at DS, and FLK Zinj (modified from Cobo-Sánchez 2020).

Abb. 7: Dreiecksdiagramm, das die Sterblichkeitsmuster für mittelgroße Boviden zeigt, die von Löwen, Hyänen, Geparden, Leoparden, Wildhunden und Jägern und Sammlern der Hadza und Kua getötet wurden (unter Verwendung von Daten aus Bunn und Pickering 2010 und Bunn und Gurtov 2014), sowie die Sterblichkeitsprofile, die bei DS und FLK Zinj dokumentiert sind (modifiziert nach Cobo-Sanchez 2020).

Table 5: Age frequency distributions of bovid MNIs at DS based on dental remains (modified from Cobo-Sánchez 2020). The actualistic carnivore and hunter-gatherer samples used for the prey mortality analysis and triangle graph (Fig. 7) stem from Bunn and Pickering (2010) and Bunn and Gurtov (2014).

Tabelle 5: Altershäufigkeitsverteilungen von Boviden-MNIs bei DS basierend auf Zahnresten (modifiziert nach Cobo-Sánchez 2020). Die für die Beutesterblichkeitsanalyse und das Dreiecksdiagramm (Abb. 7) verwendeten aktualistischen Carnivoren- und Jäger-Sammler-Stichproben stammen aus Bunn und Pickering (2010) und Bunn und Gurtov (2014).

Taxon	MNI	Young	Prime	Old
Kobus sigmoidalis	11	3	6	2
Parmularius altidens	4	3	1	
Connochaetes sp.	4		4	
Megalotragus sp.	2		2	
Tragelaphus strepsiceros	2	1	1	
Antidorcas recki	5	3	2	
Total	28	10	16	2

from confrontational scavenging from felids, stealing carcasses from felid kills that may have lacked viscera and hindlimbs (Fig. 6). Yet, the bias in the representation of front and hind limbs is not necessarily explained by confrontational scavenging. It could also be related to transport distance or simply to variability in hominin transport decisions, and does not exclude hunting.

This means that the detected evidence that could be pointing to confrontational scavenging is inconsistent and ambiguous. For instance, the uneven representation of front and hindlimbs in medium-sized carcasses could mean that hominins butchered and discarded hindlimbs at the kill site, since they have higher return rates and are more efficiently processed, as a strategy to maximize their individual energetic gain and minimize transport load. This behavior would also render the documented skeletal profiles at DS. Regardless, this only affects a small portion of the assemblage; carcasses seem to have been predominantly acquired complete by hominins.

When using the triangle graph, mortality profiles from DS and FLK Zinj overlap partly with one of the age profile samples created by lions and with the FLK background sample. According to this graph, both felids and humans can create very similar mortality patterns that resemble the structure of a living population and show a predominance of prime adults. The mortality profiles from Alcelaphini at DS and one of the lion samples match (Cobo-Sánchez 2020). There is a possibility that alcelaphines from DS were acquired through confrontational scavenging from lions, also given the high variability in age mortality profiles generated by lions (and humans). Yet, as mentioned above, the taphotypes from DS do not overlap with those typical for felids in any case, and overall, the bovid age profiles documented at the site are more similar to mortality profiles created by humans than by felids. Confrontational scavenging could therefore have been part of the hominin behavioral repertoire but, according to the DS data, not the predominant one.

Collective animal carcass consumption in central-provisioning places

A central place has been defined as a locus used repeatedly, to which resources are transported and processed, acting as the focal point of group fission/fusion (Marlowe 2010). The use of the location as a central place would be supported by the presence of local and non-local taxa and a significantly higher bone density at the site than in the surrounding landscape. Additionally, bone clusters should be qualitatively different from those at non-anthropogenic sites, and the accumulation should involve multiple individuals. Presumably, skeletal part profiles would be relatively unbiased. The environmental context of the location would be characterized by low trophic dynamics. A central place would also be characterized by food surplus that would enhance food sharing and evidence of other activities not related to animal carcass consumption. The depositional time should be short (no more than one or two years).

At DS, the high bone density inside the site contrasts significantly with the surrounding landscape, and the assemblage is formed of multiple butchered carcasses belonging to both autochthonous and allochthonous taxa. Taphonomic evidence regarding the site's integrity excludes the possibility of the accumulation being a death site or the result of natural processes. According to the site formation analysis, the DS archaeofaunal accumulation is autochthonous and undisturbed. Bones show no preferential orientation, and bone shape and composition representation is similar to that of undisturbed assemblages. There is a high degree of fragmentation of the assemblage as opposed to the high percentages of complete bones found in natural assemblages (Cobo-Sánchez 2020). Additionally, the bone clusters are also spatially different from those at non-anthropogenic sites, in essence because they are associated with lithics clusters. The clusters of stone tool debris suggest that aside from butchering, knapping activities took place at DS.

The transport of complete or partial fleshed sections of animals larger than 100 kg (including access to it and initial butchery to be transported) requires the joint participation of several individuals according to carcass size. Moreover, the collective transport of lithic raw material is also inferred, because the amount of lithic artifacts at the site exceeds the physical capability of having been accumulated by one single individual, provided that the accumulation took place mostly in one occupational episode and not across a diachronic sequence of various occupational episodes, as is the case of DS. Abundant lithic raw material exceeding the transport capacity of one individual also refers to anticipation of future needs as reflected in raw material procurement and exploitation and is linked to the reduction sequence concept (Diez-Martín et al. 2021, 2022).

There are abundant axial remains that even appear spatially distributed in six to eight clusters and that show that several carcasses were complete when they were introduced into the site and consumed collectively in reduced areas. The spatial distribution of all butchering-related activities also shows that carcasses were completely butchered in the same spots (Cobo-Sánchez 2020).

The environmental context of the location is characterized by a low to moderate competition and trophic dynamics, as indicated by low to moderate degree of ravaging at the site, and the depositional time does not exceed two or three years, as evidenced by the subaerial weathering

stages on the bone surfaces. All these arguments support that DS was used as a central provisioning place for food processing and consumption and stone tool manufacture.

The redundancy in the aforementioned butchery patterns and the representation of resources that clearly exceed the needs of one individual, especially if occurring on the same spot repeatedly, suggests that the purpose of such behavior and use of a central place could have been food sharing.

Discussion

Some authors have argued that hominin carnivory and hominin predatory behaviors evolved gradually from passive scavenging strategies for the obtainment of flesh scraps from felid kills by Oldowan hominins toward consistent early access to carcasses during the Acheulean (e.g., Cachel and Harris 1998; Holliday 2012; Pobiner 2016). Yet, the results of the taphonomic analysis of DS site show that hominins were successful and regular hunters at least 2 Ma ago, and small and medium-sized carcass foraging seem to have emerged as part of a set including other behaviors, like food sharing and cooperation (Pickering and Domínguez-Rodrigo 2010; Domínguez-Rodrigo and Pickering 2017). Interestingly, whenever a strong anthropogenic input is inferred in early Pleistocene archaeofaunal assemblages, the taphonomic evidence points every time to early access to carcasses by hominins, even in older periods in which this evidence in the archaeological record is even more scarce. For example, evisceration marks have been identified at Gona (Ethiopia) at 2.6 Ma (Domínguez-Rodrigo et al. 2005), and at Ain Boucherit (Algeria), which is dated to 2.4 Ma (Sahnouni et al. 2018). It is true that the evidence is not sufficient from 2.6 to 2 Ma to make inferences beyond tentative early access to carcasses, but the subsequent concentrations of lithic artifacts and fossil bones dating from 2.0 Ma and 1.8 Ma like DS and FLK Zinj, which also coincide with the appearance of *Homo ergaster* (Domínguez-Rodrigo et al. 2015a; Villmoare et al. 2015), allow us to test more assumptions and reconstruct a clearer picture of hominin foraging strategies.

At DS, the results from the bovid age profile analysis support hunting, more specifically (but not exclusively), ambush hunting, mainly because the documented mortality profiles fall inside the range of the age structure of a living population, with a predominance of prime adults, which constitute around 60 to 70% of the medium-sized bovid sample. When it appears in the archaeological and ethnographic record, this pattern is usually associated with selective ambush hunting (e.g., Stiner 1990; Bunn and Pickering 2010). Exactly the same tendency is observed at FLK Zinj for both carcass sizes, especially when using four age classes instead of three. The tendency to hunt high-ranked prey at these early sites also supports that hominins were already efficient hunters, as opposed to the view that their hunting capabilities evolved gradually over the Middle to Upper Pleistocene. Incidentally, hunting scenarios are accepted for several other Lower Paleolithic sites in Eurasia based on similar evidence. Other significant assemblages that are interpreted as the result of hunting are TD6-2 at Gran Dolina in Atapuerca (~0.80 Ma; Saladié et al. 2011, 2014) or the assemblage of fallow deer in Gesher Benot Ya'aqov in Israel (~0.75 Ma;

Rabinovich et al. 2008). At TD6-2 all age groups are represented, but the profile is dominated by immature and adult individuals (Saladié et al. 2011, 2014). Gesher Benot Ya'aqov constitutes an assemblage dominated by a single taxon (*Dama dama*) where adult individuals are most abundant (Rabinovich et al. 2008). At TD10.1 at Gran Dolina in Atapuerca (dated to around ~350 ka), prime-adult individuals dominate the deer mortality profile also. This site represents a long-term residential base camp formed probably by very intensive occupations. This preference on high-ranked prey is similar to that documented in other Middle and Late Paleolithic sites across Europe and the Levant (Rodríguez-Hidalgo et al. 2015, 2017) and coincides with the prey selection profile that is interpreted as unique for humans (Stiner 1990). If we accept the age mortality profiles from these sites and more recent periods as evidence of hominin predatory behavior, the same should apply for earlier anthropogenic sites, especially if they appear coupled with taphonomic evidence for early access, as is the case of DS.

Age profiles are not the only line of evidence with similar outcomes at DS and at sites from other more recent periods. In fact, one of the most important results obtained in the present study is precisely that several aspects of the taphonomic pattern yielded by the faunal assemblage at DS, in particular the frequencies and location of cut marks, do not differ from those obtained from sites from substantially later periods, where hunting is undisputed. The previously mentioned assemblages are also a good example thereof, because they have been studied thoroughly from a taphonomic perspective. Similar as to what can be observed at DS, in these assemblages there is evidence for the performance by hominins of all butchering-related activities, which again establishes that hominins had early access to abundant meat resources. For example, skinning is evidenced by cut marks on the crania, the metapodials and the phalanges. Detachment of the crania from the postcranial skeleton by cut marks on atlases and cut marks (and in some cases also hack marks) on epiphyses of long bones reveal disarticulation activities. Evisceration is demonstrated by abundant cut marks on the ventral sides of ribs and some vertebrae, and intensive defleshing is evidenced by high percentages of cut (slicing) marks on hot zones of meaty long bones. This demonstrates that carcasses were completely and efficiently processed regularly at these sites, following the same butchery patterns that are also typical in later periods of human evolution (e.g., Rabinovich et al. 2008).

The bovid age profiles and the taphonomic and zooarchaeological similarities between DS and other early Pleistocene sites where hunting is accepted are the most important arguments stemming from this study in favor of an early human predatory behavior. However, the fact that the mortality profiles from DS do not consistently overlap with those typical for felid kills is equally important, although occasional overlap is documented with the age profiles created by lions when using three age classes or when using five age classes and considering only the *Alcelaphini* subsample. However, this match must be taken cautiously, first because lions produce very variable bovid age profiles depending on certain environmental aspects and seasonality, and secondly, because in the case of DS, these similar profiles do not appear in conjunction with typical felid damage on the bones. The almost complete absence of this type of damage patterns

in the faunal remains of DS argues against scavenging (passive or confrontational). If most carcasses accumulated at DS were the result of aggressive scavenging from felids, these bone modification patterns should be more commonly documented.

Evidence from other Bed I sites like FLKN 1-6, FLK 10-15, DK and FLKNN, where hominins do not seem to have taken advantage of large amounts of complete bones from felid accumulated remains, should not be disregarded. At these sites, complete bones were left unprocessed by hominins. For example, at FLKN 1-6 hominin activity is documented by the presence of lithics in every level of the long sequence spanning hundreds or thousands of years, yet they do not seem to have engaged in exploiting the remains of felid kills. This suggests that scavenging from felids was not a common activity, although the possibility that occasional scavenging may have happened should not be excluded. Even if the mentioned taphonomic signals were reflecting power scavenging, the patterns are not consistent. The taphonomic signal should be more accentuated if the bulk of the assemblage had been acquired through aggressive scavenging. By contrast, the factors pointing to hunting are much more consistent. Thus, it is probable that hunting was the predominant strategy used by hominins to obtain large quantities of meat already by 2–1.8 Ma ago.

Aside from determining the degree of involvement of hominins in carcass acquisition and meat consumption at early sites, the evidence from DS shows that some early sites were created by hominins repeatedly carrying animal carcasses and stones to particular places in the landscape. The concept of 'central place' entails that these places also had a social function in addition to being used for specific activities related to subsistence. This means that hominins could have used these places for sharing food and therefore have stayed at these locations for prolonged periods of time, rather than only have used these spots sporadically as refuge places or stone caches when trying to avoid predation risk.

The possibility of using central places repeatedly for hominin activities would be conditioned on the one hand by the amount of food surplus available for hominin consumption, a condition met in the case of DS, and on the other hand by the degree of carnivore predation risk in the surroundings of the site (Blumenschine 1991). Carnivore competition or predation risk can be assessed by means of reconstructing the paleoenvironment in which the site was formed and by establishing the degree of carnivore ravaging at a site, which can be used as a proxy for carnivore competition. The taphonomic analyses of the Bed I sites showed that carnivores were very active in the lacustrine plain of the former Olduvai lake where these sites formed. Some felids, like leopards, *Dinofelis*, and solitary lions, were accumulating carcasses at certain locations, probably seeking low-competition settings. The predatory guild was very diverse compared to the carnivore species that are found in modern savannas today, which also suggests that competition among carnivores must have been significant (Domínguez-Rodrigo et al. 2007). Sites were probably located in transitional zones between the alluvial plain and the lacustrine floodplain in closed-vegetation habitats (lacustrine forests), which were probably relatively low-competition habitats (Domínguez-Rodrigo et al. 2007). DS and FLK Zinj were located on a topographically higher platform in a wooded environment dominated by palm and acacia trees

(Uribelarrea et al. 2014; Arráiz et al. 2017). These wooded environments would have represented the lowest competition areas, which explains why hominins would have selected these loci for their activities. The analysis of several skeletal part ratios to estimate ravaging intensity also suggested that the degree of ravaging and carnivore competition were low to moderate at DS. More intensive ravaging is documented at FLKN and DK, which formed in a more open environment. The same inferences can be drawn from bovid taxa representation at the sites. While more species from mixed habitats such as waterbucks (Kobus) are predominant at FLK Zinj and DS, bovids from more open environments, like *Antidorcas* and *Parmularius* are dominant at FLKN (Domínguez-Rodrigo et al. 2007). The few individuals belonging to these taxa represented at DS were probably carried across longer distances and brought into the sites from further than the immediate vicinity of the site.

High degrees of carnivore competition could have had consequences regarding scavenging opportunities for hominins. If carnivores were very active in the Olduvai Bed I environment, the opportunities for passive scavenging would have been very low. In addition, since confrontational scavenging is a riskier activity than hunting, it is possible that carnivore predation could have posed a major threat for hominins, as they do for modern foragers still today (Treves and Naughton-Treves 1999). Yet, the risk of carnivore predation could have likewise promoted higher cooperative behaviors among hominins and increased sociality, as is observed in fact in several extant primate species (Rose and Marshall 1996).

Bone remains and lithic artifacts at PTK and AGS present similar taphonomic signatures and seem to be also spatially distributed in large clusters of similar characteristics as the ones from FLK Zinj and DS, which could suggest that these sites could have been selected by hominins for similar purposes (work in progress). This does not preclude the use of other locations in the Zinj paleolandscape by hominins for other activities. The palimpsests formed at other Bed I sites show that hominins were active in other loci as well. The existence of at least three central places in the Zinj paleolandscape in a relatively small area (around 1000 m²) suggests that hominin groups were very active in the area, just like carnivores. The floodplain, with several (seasonal) fluvial input areas and the nearby location of a freshwater spring could have been an important area of attraction for many species of herbivores, given the presence of accessible water resources.

Conclusions

The taphonomic study of DS supports previous interpretations about hominin behavior drawn from earlier taphonomic analyses of FLK Zinj, as well as the high explanatory power of the applied taphonomic and spatial approaches. In particular, the results show that the faunal assemblage from Level 22B at DS is an autochthonous largely undisturbed assemblage and that complete fleshed small and medium-sized ungulate carcasses were actively transported and introduced into the site by hominins. These had early access to meat resources. The evidence also points to hunting as the main carcass foraging strategy employed by early humans, probably through ambush techniques, and suggests that carnivore activities were limited at the site. DS

seems to have been used by hominins as a central place near locations with easy access to herbivores and water sources. At these places, hominins probably congregated on small areas and consumed food collectively. The regular successful acquisition of large carcasses and their transport to central places likely relied on high levels of group cooperation. The evidence from DS indicates that early *Homo* showed significant behavioral complexity relative to extant primates and a very cohesive social structure.

These interdependent behaviors inferred from DS and FLK Zinj are probably attributable to *Homo ergaster* or to a similar species. Therefore, the results are also in line with the general agreement among researchers that the appearance of this species marked a significant shift in adaptation from the other hominins. Around 2 Ma ago, the consumption of meat by hominins increased significantly, and a number of socio-reproductive behaviors that enabled and required meat-eating were also adopted. At that time, hominins appear to have already been part of the predatory guild and very successful hunters. The early archaeological record shows that in spite of their limited technology and their smaller brains compared to those of modern humans, early humans were capable of certain cognitively complex behaviors, including anticipating adaptive needs, and were well-adapted to certain forms of hunting and group cooperation, even though their predatory behaviors and social reproductive structures may not have an equivalent in the present.

Acknowledgments

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