A case of hominin scavenging 1.84 million years ago from Olduvai Gorge (Tanzania)

Manuel Domínguez-Rodrigo, Lloyd A. Courtenay, Lucía Cobo-Sánchez, Enrique Baquedano, and Audax Mabulla

1 Institute of Evolution in Africa (IDEA), Alcalá University and Regional Archaeological Museum of Madrid, Madrid, Spain. 2 Area of Prehistory (Department History and Philosophy), University of Alcalá, Alcalá de Henares, Spain. 3 Department of Anthropology, Rice University, Houston, Texas. 4 Department of Cartographic and Terrain Engineering, Higher Polytechnic School of Ávila, University of Salamanca, Ávila, Spain. 5 Computational Archaeology (CoDArchLab), Institute of Archaeology, University of Cologne, Cologne, Germany. 6 Regional Archaeological Museum of Madrid, Plaza de las Bernardas s/n, Alcalá de Henares, Spain. 7 Department of Archaeology and Heritage Studies, University of Dar es Salaam, Dar es Salaam, Tanzania

Address for correspondence: Manuel Domínguez-Rodrigo, Institute of Evolution in Africa (IDEA), Alcalá University, Covarrubias 36, Madrid, 28010, Spain. manuel.dominguezr@uah.es, mdr@rice.edu

Meat eating is one of the hallmarks of human evolution. It has been linked to the beginning of stone tool use, to physiological changes leading to crucial anatomical transformations defining our genus, and to new socio-reproductive and cognitive behaviors. Uncontroversial evidence of meat eating goes back to 2.6 million years ago; however, little is known about the frequency and timing with which early hominins acquired animal resources. Here, we show that the combination of hunting and scavenging documented in some modern human foragers may have a long evolutionary trajectory. Using a new set of artificial intelligence methods for objective identification, we present direct evidence of an episode of hominins scavenging from large felids—probably lions—discovered at Olduvai Gorge (DS site, Bed I). This casts a new perspective on the diversity of hominin carcass acquisition behaviors and survival strategies, and places some early Pleistocene hominins in ecological proximity to African large carnivore guilds.

Keywords: human evolution; meat eating; scavenging; taphonomy; machine learning; Pleistocene
early Pleistocene archaeological record has been based on indirect evidence (i.e., damage left by nonhominin carnivores on bones), instead of direct evidence of overlap of carnivore and hominin traces on the same fossils.\textsuperscript{17–20} The nature of the indirect evidence has been controversial and some interpretations have neglected the behavioral information provided by the cut-marked portions of early archaeofaunal assemblages.\textsuperscript{21–28} Additionally, a substantial amount of purported carnivore damage upon which these interpretations are based has been contested as being caused by bioerosion.\textsuperscript{29–31}

Potential overlap on the same fossils of carnivore tooth marks and hominin-imparted cutmarks was documented at some sites in Olduvai Gorge (Tanzania).\textsuperscript{32,33} However, such evidence is inconclusive because trampling marks crossing tooth marks may have been misidentified as cut marks.\textsuperscript{31} Furthermore, these interpretations of BSMs are based on subjective assessment by experts, which has limitations.\textsuperscript{34} To date, no objective assessment of BSM on early Pleistocene bone specimens bearing a palimpsestic combination of hominin-imparted cut marks and carnivore-specific tooth marks has been scientifically supported.

To address this problem, we applied artificial intelligence and machine learning tools—currently the most objective methods—to classify BSM. These methods enabled the identification of a felid–hominin interaction from the early Pleistocene site of DS (David’s Site) from Olduvai Bed I: the first direct evidence that scavenging was, alongside hunting, part of the behavioral repertoire of early Homo.

**Methods**

For the present analysis, a new set of methods for objective identification of BSM has been used to minimize the probability of error (see detailed description of the methodology used and samples evaluted in Supplementary Information, online only). Briefly, single meta-layer, multiple meta-layer stacking, and average majority voting ensemble learning methods were applied to a selection of...
Figure 2. (A) Microscope image (30×) of the percussion mark shown in (B) (scale = 1 cm). Medial (C), frontal (D), lateral (E), and caudal (F) aspects of the DS16-4287a radius. Sf, spiral fracture.

Results

The DS16-4287 right radius-ulna belongs to a medium-sized alcelaphine bovid slightly smaller than modern wildebeest (*Connochaetes taurinus* (i.e., *Parmularius*)), and was discovered at the 1.84 Ma site of DS (Bed I, Olduvai Gorge). Both elements were discovered articulated during excavation in proximity to the only articulated axial skeleton (vertebrae plus ribs) found at the site. DS is found in the same thin clay stratum as FLK Zinj (where OH5, the holotype of *Paranthropus boisei* was discovered) and pene-contemporaneous with it.38 The ulna (DS16-4287b) presents modifications in the form of minor furrowing on the proximal rim of the olecranon and a couple of isolated tooth pits on the olecranon body (Fig. 1). This is typical of modern lions.39,40 The large size of these tooth marks (major axis = 6.9 and 6.5 mm, respectively) fit the 95% confidence interval of lion and spotted hyena tooth marks on epiphyseal portions among all of the extant carnivores adapted to African biomes.41,42 When hyenas modify ulnae of medium-sized carcasses, they ravage the olecranon intensively, in most cases making it disappear, and if tooth marking occurs, it is conspicuous and abundant (see Fig. S5, online only). This is typical of durophagous carnivores.43

The minor furrowing of DS16-4287b, the preservation of the olecranon almost complete, and the occurrence of only two tooth marks is indicative of felid rather than hyenid modification (see Fig. 1D).40,43 These inferences are confirmed by the use of deep learning computer vision, which, with an accuracy of 100% on testing experimental samples, identified both tooth pits on this ulnar specimen as caused by lions (Table S8, online only).

In addition to carnivore damage, hominin damage is documented in the form of a percussion mark and several cut marks. The radius (DS16-4287a) exhibits a green spiral fracture typical of hammerstone-imparted dynamic loading. Associated with the fracture is a percussion mark on the medial side (Fig. 2). This mark is elongated with pointed ends, typical of the use of modified hammerstones.44 In addition, eight V-shaped BSM with parallel oblique orientation are documented on the lateral-cranial side of the metadiaphysis (Fig. 3). The location of the marks almost excludes their
creation by trampling, since the radius almost always rests on the cranial-caudal sides on the ground because of their greater width. The preservation of these marks is not pristine, since the outer cortical layer has been exposed to some degree of chemical modification and manganese staining appears on the bone surface in the form of small patches. Etching and flaking are documented in some parts of the specimen, affecting also portions of some of the marks. Chemical cracking is also observed. Despite this, when scrutinized through deep learning computer vision, all eight marks were classified as cut marks, and six of the BSM as cut marks with high confidence—five of them with a probability higher than 90% (Table S7, online only). Using geometric morphometric-based ensemble learning techniques with the three-dimensional models of these BSMs (Fig. 4), at least four of the same marks were classified as cut marks also with high confidence, despite the intensive morphing of the fossil because of the impact of diagenesis on the bone (Table S6, online only). Fortunately, most of the damage impacting parts of the fossil surface did not affect most marks and all of them can be classified as well preserved or as mostly well-preserved, with diagenesis affecting only a small portion of the trajectories of a few (Fig. 3). This enabled the preservation of most of the original microscopic features in all the marks analyzed, even if these microfeatures might not be visible in some portions. As explained in the Methods section above, the high augmentation used in the present study prevented the simultaneous analysis of the complete mark and focused, therefore, on the best preserved parts thereof, so that proper comparison with the experimental marks could be made.

From the collected data, we conclude that several marks (a minimum of four and a maximum of eight) analyzed on DS16-4287a are stone tool-imparted cut marks. Such anthropogenic agency is further supported by the presence of the percussion mark in the vicinity of the spiral fracture caused by green breakage, as described above. The presence of lion modifications on a cut-marked and hammerstone-broken element shows that the order of consumption was that lions had first access and hominins intervened afterward (see below).

Discussion

In the initial stage of the hunting-scavenging debate, it was assumed that hominins could be marginal scavengers, opportunistically exploiting meagre resources even after strict carnivores and durophagous fissipeds had accessed carcasses before them. Subsequent actualistic work with carnivores in African ecosystems showed that...
hominins could only carve a scavenging niche if they acquired felid kills before durophagous carnivores intervened.\textsuperscript{12–14} The latter are terminal scavengers. Barely anything remains after their intervention. Since then, the two scenarios considered to interpret early archaeological sites were either dual-agent (hominin–hyenid)\textsuperscript{21–31} or multiple-agent (felid–hominin–hyenid).\textsuperscript{17–20}

Within the latter opportunistic scenario, models considered hominins passively scavenging largely defleshed carcasses from felid kills\textsuperscript{17–19} or actively snatching them through confrontation.\textsuperscript{2,22,27,31,33,46} Scavenging models inferred from the early Pleistocene archaeological record have been based mostly on the action of nonprimate carnivores (i.e., analysis of frequency of tooth marks, assuming that none of those were made by hominins), and not on hominin behavior (i.e., the anatomical distribution of cut marks resulting from stone-tool butchery).\textsuperscript{17–19} The discovery that largely more than two thirds of the purported tooth marks at FLK Zinj were bioerosive\textsuperscript{20,21,29} removed heuristics to the interpretation of the carnivore input at the site, and to opportunistic behaviors of early humans. The revised assessment of the purported hominin traces overlying carnivore tooth marks\textsuperscript{32} also showed that these resulted most likely from abrasion modifying tooth marks, not from cut marks.\textsuperscript{21}

The application of artificial intelligence tools (as we can see in the present work) to the traces

---

**Figure 4.** Orthophotograph and microtopographical data derived from digital elevation models of two regions of interest (ROI) of the DS16-4287a radius. (A) ROI for marks BSM1 (cross-sections I and III) and BSM2 (cross section II). (B) ROI for marks BSM7 (cross-sections I and II) and BSM8 (cross section III).
made on bone surfaces by hominins and carnivores has contributed to overcome the impasse in which defenders and detractors of both hypotheses were, using virtually the same arguments over decades. The recent application of computer vision deep learning algorithms to DS, much more capable than human experts in objectively discerning human and nonhuman agency in bone modifications, has revealed that all the reliably identified tooth marks at the site were made by hyenids and not felids, with the exception of the carcass to which DS16-4287 belongs (submitted). This emphasizes again primary access by hominins to fleshy animals for most cases.

A wealth of taphonomic information created by hominins themselves is contained in the frequency and anatomical distribution of cut marks created during butchery. Recently, a comparative 3D anatomical distribution of cut marks at DS and the other two pene-contemporaneous sites of FLK Zinj and PTK, occurring on the same paleoscape, has shown an interesting patterning in how cutmarks are anatomically distributed in the three assemblages. The anatomical distribution is only coincident with experimental butchery of complete animals, and not with experimentally butchered carcasses obtained from felid kills with different degrees of intensity in their consumption. The overall picture reinforces interpretations of early access of hominins to most of the carcasses represented at those sites. The existence in all of these sites of evisceration cut marks on the ventral sides of ribs and vertebrae further shows that carnivores did not predate hominins in their access to those carcasses, since viscerae are the first parts of carcasses consumed by felids. This is why the discovery of the DS16-4287 radius–ulna is of importance, because contrary to all previous efforts in attributing opportunistic behaviors to hominins indirectly through the reading of the input of carnivores, it clearly shows a felid and a hominin signal on the same limb portion that can be identified to specific agency. What are the possible options for such combined modifications on the same carcass?

Scenario 1: hunting by hominins, followed by scavenging by lions
Scenario 2: hunting by lions followed by passive scavenging by hominins
Scenario 3: hunting by lions followed by active, confrontational scavenging by hominins

Scenario 1 can be tested against the butchery actions of hominins recorded on the carcass, and the specific modification created by the felids. Hominins removed the bulk flesh from the radius as reflected in the location of the cut marks along the proximal lateral shaft. No muscle insertion lies in that part, and butchery experiments show that marks imparted there are more likely to be the result of defleshing rather than dismembering. The percussion mark on the medial portion of the shaft must, therefore, have been made during the hammerstone impact on the defleshed bone surface. This is attested by the green breakage associated with it. The shaft would not have broken like that if flesh was overlying the bone and buffering the impact of the hammerstone. All this implies that the radius–ulna were defleshed upon discard by hominins. Felids, and more specifically lions, show no interest in defleshed carcasses, because as strict carnivores they do not consume the grease embedded in cancellous epiphyseal bone. This is why they abandon marrow and grease bearing long bones mostly intact after carcass consumption.

In addition, the typical furrowing on the ulnar olecranon imparted by felids during carcass consumption takes place during the extraction of the distal humeral flesh, resulting in the joint modification of the olecranon and the medial humeral epicondyle. Lions have never been documented to impart this modification on the ulna when the olecranon is already exposed and the humerus totally defleshed, or both humerus and radius–ulna are already disarticulated. All this together makes the hominin–lion sequence highly unlikely at DS. Scenarios 2 and 3 are more feasible. Scenario 2 would require that hominins had accessed the carcass after lion consumption, resulting in a largely defleshed limb. Hominins would then have demarrowed the radius, creating the percussion

---

*It should be emphasized that the previous taphonomic approach of assessing the impact of felids in archaeofaunal assemblages was extremely subjective, because in no instance could the specific agency (i.e., felid or hyenid) be assessed through the determination of frequency or metrics of tooth marks.*
We had hominins repeat this research. Although Klepto-parasitism of these scavengers is not well studied, we can provide some insight into this behavior. A case of hominin scavenging has been documented, and it may be due to this opportunistic strategy being so infrequent as to leave few traces on bones.

The discovery of DS16-4287 shows that scavenging (i.e., felid–hominin interaction) can be demonstrated, when it exists, through direct evidence of damage imparted by both agents on the same bones. At 1.84 Ma, hominins at Olduvai exploited medium-sized carcasses more abundantly than those of other sizes. Klepto-parasitism of these carcasses would theoretically be feasible at lion kills and at those of other similarly sized felids. Lions exhibit a pattern of damage to the appendicular skeleton of their prey. Had hominins repeatedly obtained carcasses from felid kills, one would expect an abundance of direct evidence of traces of felids and hominins (like those presented here) on the same bones from archaeofaunas unearthed at early Pleistocene sites. The dearth of this type of direct evidence can only indicate that such an opportunistic behavior was probably marginal or infrequent enough to be archaeologically hard to detect.

In contrast, the most parsimonious way to reconcile taphonomic evidence of cut, percussion, and tooth marks on the anthropogenic sites from Olduvai Bed I is the interpretation that hominins were focusing on bulk flesh exploitation. Although this is suggestive of either hunting or confrontational scavenging, no direct evidence has been presented before to support either of them. The case reported here could also suggest hominin access to a partially fleshed carcass upon premature abandonment by felids (including sabertooths). We believe this is more unlikely than our conclusion because, for medium-sized carcasses, lions in modern African natural ecosystems abandon most of their prey when mostly or completely defleshed.

Available evidence of Homotherium consumption of carcasses also indicates efficient defleshing of prey by sabertooth felids. A recent taphonomic analysis of a Xenosmilus den also shows thorough defleshing of carcasses by that prehistoric sabertooth homotherine predator (submitted).

Our interpretation of early access to carcasses by hominins is further supported by the mortality profiles of the medium-size ungulate fauna unearthed at the site (see Supplementary Information, online only).

One study suggested that the modern Hadza foragers in Tanzania might obtain up to 20% of their consumed resources from medium-sized and large carcasses from actively confronting felids. This is far more than documented for other African foragers, probably due to the combination of use of poison on metal arrowheads dispatched with long bows. This enables the Hadza to attempt confrontational scavenging from a distance when snatching prey from lions. This study shows, though, that except for one intact carcass and four that were partially defleshed upon encounter (with viscerae and upper limb flesh removed), the remainder of carcasses documented were “heavily ravaged by carnivores” with most defleshing having taken place.

Until present, no lion damage has been documented in any Hadza-accumulated faunal assemblage. This may be due to this opportunistic strategy being so infrequent as to leave few traces on bones. It may also be the result of lack of taphonomic studies, because felid bone damage patterns have only been recently documented, and most Hadza faunal studies published are substantially older. A reanalysis of Hadza scavenged carcasses would enable differentiating among these options. In the event of lack of felid modification on these carcasses, this would be indicative of a fairly fleshed state of carcasses when acquired by the Hadza. This would contrast with the observation above that most carcasses are partially defleshed when found by the Hadza. We foresee the opposite. We believe that a reanalysis of the Hadza-consumed faunal assemblages will yield evidence of this behavior. For a carcass to be modified as in the case of DS16-4287, using the regular carcass consumption behavior reported for felids as an analog, this would imply a substantial defleshing prior to human (hominin) access. Studies on the prey consumption sequence by lions show that for the ulnar olecranon to be furrowed like that, the humerus must have been defleshed. Humeri commonly follow the internal rib cage and the
proximal hindquarters in the defleshing sequence by lions.\textsuperscript{12}

The presence of cut marks on the DS16-4287 proximal radius–ulna shaft shows that hominins did not acquire the carcass when it was mostly or totally defleshed upon abandonment, since flesh scraps do not commonly survive on the portion where the cut marks are found.\textsuperscript{48} The bulk defleshing of this anatomical part by hominins indicates an intermediate to early access.\textsuperscript{14} This would be suggestive of confrontational rather than passive scavenging.

Only two other cases of felid-modified bones have been reported from another anthropogenic site at Olduvai (FLK Zinj).\textsuperscript{40} They were unbroken and unmodified by hominins. They could result from palimpsestic independent deposition by felids\textsuperscript{55} or by hominins having skillfully bulk-defleshed them without demarrowing. This is of relevance because proximal radius–ulnae are abundant in the Olduvai archaeological record. Experimental studies on lion-consumed carcasses show that proximal radii–ulnae and proximal humeri are the most intensively damaged long bone portions,\textsuperscript{21} spanning from about 25% to 100%\textsuperscript{14,21,39} of these portions.

At the Olduvai Bed I anthropogenic sites of FLK Zinj, DS and PTK, there are 72 proximal radii–ulnae from hammerstone-fragmented elements and only the specimen reported here bears clear damage inflicted by felids.\textsuperscript{21} This means that only 2.7% (if including the complete radius–ulna described above) of the preserved ulnar specimens bear felid modifications, an order of magnitude exponentially inferior to the minimum range experimentally documented among lions. This indicates that scavenging did not provide the bulk of carcasses documented among modern Hadza, but also what characterizes behaviors of some top predators, like lions, which may scavenge up to 16–25% of what they eat,\textsuperscript{56} substantially more than what is documented at the anthropogenic Bed I sites.

\section*{Acknowledgments}

We thank the Spanish Ministry of Science and Innovation for funding this research (PID2020-115452GB-C21). We also thank the Ministry of Culture and Sport for funding through the program of archaeological projects abroad. We also thank NCAA (Ngorongoro Conservation Area Authority), the Antiquities Department, and COSTECH (Commission for Science and Technology) for their permission to conduct research in Tanzania. L.A.C. is funded by the Spanish Ministry of Science and Innovation, with an FPI Predoctoral Grant (Ref. PRE2019–089411) associated with project RTI2018–099850–B–I00. Furthermore, we also thank Blanca Jiménez-García and Natalia Abellán for their work with lions and hyenas and for sharing the images of tooth marks. We also thank Gabriel Cifuentes-Alcobendas and Marcos Pizarro for their experimental work and for sharing their images of cut and trampling marks. We are indebted to the comments made by J. Parkinson, A. Val, and an anonymous reviewer of an earlier draft.
of this manuscript. We are especially thankful to D. Braaten for his constructive editorial suggestions.

**Author contributions**

M.D.-R. and L.C.-S. analyzed the fossils. L.A.C. contributed the experimental sample for 3D images. The three authors conducted the computational analysis. All five authors wrote the paper.

**Supporting information**

Additional supporting information may be found in the online version of this article.

**Table S1.** Minimum number of individuals represented by mandibular elements at DS, which are more abundant than maxillary elements and provide thus a more accurate estimate of the number of individuals represented (Level 22B).

**Figure S1.** (A) Kernel density map of axial (ribs and vertebrae) elements, with Trench 39 highlighted. (B) Detail of articulated axial skeleton in Trench 39 from the alcelaphini carcass to which the radius–ulna DS16-4287 belongs.

**Table S2.** Algoritms and parameters used for base learning.

**Table S3.** Stacked EL models and their results.

**Table S4.** Neural network architectures used for the EL stacking model.

**Table S5.** Majority voting models and their results. Key: Rf, random forest; et, extremely randomized trees; gbm, gradient boosting machine; lr, logistic regression; cb, categorical boosting; CV, cross-validation. For the “nn” models, see Table S3.

**Table S6.** Classification of the DS marks (numbered as in Fig. 3 of the main text).

**Figure S2.** BSM7 documented with binocular microscope (30×) classified as cutmarks with 99% probability by the CNN model.

**Table S7.** Probability of classification of each of the images for marks BSM1 to BSM8 using the VGG16 CNN model and final classification of each of them.

**Figure S3.** Radii–ulnae of equids ravaged by spotted hyenas.

**Figure S4.** Ulnae of a zebra and a wildebeest with intense modification of olecranons by lions.

**Figure S5.** Furrowing on the proximal rim of the olecranon and associated tooth scores and pits by lions.

**Figure S6.** The two tooth pits documented on the DS16-4287b ulna.

**Figure S7.** Dimensions of major axis for both tooth pits (pentagons) within the same 95% confidence interval of tooth pit dimensions on epiphyseal cancellous bone of lions.

**Table S8.** Probability of classification of both images for marks BSM1 (complete pit) and BSM2 (incomplete pit) using the ResNet50 CNN model.

**Figure S8.** Orthophotograph and digital elevation model derived from microphotogrammetry of the BSMs observed on the DS16-4287a radius.

**Figure S9.** 3D model examples of experimental trampling marks produced by the HIROX KH-8700 3D Digital Microscope.

**Table S9.** Description of the 3D 13-Landmark model employed in the present study, as originally described by Courtenay *et al.*, and developed for trampling mark analysis in Ref. 10.

**Figure S10.** Examples of landmark digitization procedures using 3D models derived from microphotogrammetry (A) on the DS16-4287a radius, and 3D digital microscopy (B, C) for the digitization of experimental cut marks.

**Figure S11.** Principal component analysis scatter plot of experimental cut and trampling mark morphologies in comparison with BSM observed on the DS16-4287a radius.

**Competing interests**

The authors declare no competing interests.

**Peer review**

The peer review history for this article is available at https://publons.com/publon/10.1111/nyas.14727

**References**

1. Aiello, L.C. & P. Wheeler. 1995. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* 36: 199–221.

2. Stanford, C.B. & H.T. Bunn. 2001. *Meat-Eating and Human Evolution*. Oxford: Oxford University Press.

3. Aiello, L.C., N. Bates & T. Joffe. 2001. In defense of the expensive tissue hypothesis. In *Evolutionary Anatomy of the
A case of hominin scavenging

**Primate Cerebral Cortex.** D. Falk & K.R. Gibson, Eds.: 57–78. Cambridge: Cambridge University Press.

4. Semaw, S., P. Renne, J.W. Harris, *et al.* 1997. 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* **385**: 333–336.

5. Dominguez-Rodrigo, M., T.R. Pickering, S. Semaw & M.J. Rogers. 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**: 109–121.

6. de Heinzelin, J., J.D. Clark, T. White, *et al.* 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. *Science** **284**: 625–629.

7. Harmand, S., J.E. Lewis, C.S. Feibel, *et al.* 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* **521**: 310–315.

8. McPherron, S.P., Z. Alemseged, C.W. Marean, *et al.* 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature** **466**: 857–860.

9. Dominguez-Rodrigo, M., T.R. Pickering & H.T. Bunn. 2010. Configurational approach to identifying the earliest hominin butchers. *Proc. Natl. Acad. Sci. USA** **107**: 20929–20934.

10. Dominguez-Rodrigo, M. & L. Alcalá. 2019. Pliocene archaeology at Lomekwi 3? New evidence fuels more skepticism. *J. Afr. Archaeol.* **17**: 173–176.

11. Archer, W., V. Aldeias & S.P. McPherron. 2020. What is ‘in situ’? A reply to Harmand, et al.(2015). *J. Hum. Evol.* **142**: 102740.

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

13. Dominguez-Rodrigo, M. 1999. Flesh availability and bone modifications in carcasses consumed by lions: palaeoecological relevance in hominid foraging patterns. *Palaeogeogr. Palaeoclimatol. Palaeoecol** **149**: 373–388.

14. Gidna, A.O., B. Kisui, A. Mabulla, *et al.* 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.* **322–323**: 167–180.

15. Stanford, C.B. 1998. *Chimpanzee and Red Colobus: The Ecology of Predator and Prey*. Cambridge, MA: Harvard University Press.

16. Watts, D.P., K.B. Potts, J.S. Lwanga & J.C. Mitani. 2012. Diet of chimpanzees (Pan troglodytes schweinfurthii) at Ngogo, Kibale National Park, Uganda. 2. Temporal variation and fallback foods. *Am. J. Primatol.* **74**: 130–144.

17. 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**: 21–51.

18. 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.

19. Pante, M.C., R.J. Blumenschine, S.D. Capaldo & R.S. Scott. 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**: 395–407.

20. Pobiner, B.L. 2015. New actualistic data on the ecology and energetics of hominin scavenging opportunities. *J. Hum. Evol.* **80**: 1–16.

21. Dominguez-Rodrigo, M., R. Barba & C.P. Egeland. 2007. *Deconstructing Olduvai: A Taphonomic Study of the Bed I Sites*. Springer Science & Business Media.

22. Dominguez-Rodrigo, M. 2002. Hunting and scavenging by early humans: the state of the debate. *J. World Prehist.* **16**: 1–54.

23. Dominguez-Rodrigo, M. 2008. Conceptual premises in experimental design and their bearing on the use of analogy: an example from experiments on cut marks. *World Archaeol.* **40**: 67–82.

24. Egeland, C.P. & M. Dominguez-Rodrigo. 2008. Taphonomic perspectives on hominid site use and foraging strategies during Bed II times at Olduvai Gorge, Tanzania. *J. Hum. Evol.* **55**: 1031–1052.

25. Dominguez-Rodrigo, M. 2009. Are all Oldowan Sites Palimpsests? If so, what can they tell us about Hominid Carnivory? *In Interdisciplinary Approaches to the Oldowan*. E. Hovers & D.R. Braun, Eds.: 129–147. Springer Netherlands.

26. Pickering, T.R., C.P. Egeland, M. Dominguez-Rodrigo, *et al.* 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**: 30–45.

27. Pickering, T.R. 2013. *Rough and Tumble: Aggression, Hunting, and Human Evolution*. Berkeley, CA: University of California Press.

28. Dominguez-Rodrigo, M. 2015. Taphonomy in early African archaeological sites: questioning some bone surface modification models for inferring fossil hominin and carnivore feeding interactions. *J. Afr. Earth Sci*. **108**: 42–46.

29. Dominguez-Rodrigo, M. & R. Barba. 2006. New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site: the carnivore–hominid–carnivore hypothesis falsified. *J. Hum. Evol.* **50**: 170–194.

30. Dominguez-Rodrigo, M. & R. Barba. 2007. Five more arguments to invalidate the passive scavenging version of the carnivore–hominid–carnivore model: a reply to Blumenschine, et al. (2007a). *J. Hum. Evol.* **53**: 427–433.

31. 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.

32. Potts, R. & P. Shipman. 1981. Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. *Nature* **291**: 577–580.

33. Monahan, C.M. 1996. New zooarchaeological data from Bed II, Olduvai Gorge, Tanzania: implications for hominid behavior in the Early Pleistocene. *J. Hum. Evol.* **31**: 93–128.

34. Byeon, W., M. Dominguez-Rodrigo, G. Arampatzis, *et al.* 2019. Automated identification and deep classification of cut
marks on bones and its paleoanthropological implications. J. Comput. Sci. 32: 36–43.
35. Courtenay, L.A., R. Huguet, D. González-Aguilera & J. Yravedra. 2019. A hybrid geometric morphometric deep learning approach for cut and trampling mark classification. NATO Adv. Sci. Inst. Ser. E Appl. Sci. 10: 150.
36. Courtenay, L.A., J. Yravedra, R. Huguet, et al. 2019. New taphonomic advances in 3D digital microscopy: a morphological characterisation of trampling marks. Quat. Int. 517: 55–66.
37. Domínguez-Rodrigo, M., G. Cifuentes-Alcobendas, B. Jiménez-García, et al. 2020. Artificial intelligence provides greater accuracy in the classification of modern and ancient bone surface modifications. Sci. Rep. 10: 18862.
38. Domínguez-Rodrigo, M., L. Cobo-Sánchez, D. Uribelarrea, 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: 805–815.
39. Gidna, A., J. Yravedra & M. Domínguez-Rodrigo. 2013. A cautionary note on the use of captive carnivores to model wild predator behavior: a comparison of bone modification patterns on long bones by captive and wild lions. J. Archaeol. Sci. 40: 1903–1910.
40. Parkinson, J.A., T. Plummer & A. Hartstone-Rose. 2015. Characterizing felid tooth marking and gross bone damage patterns using GIS image analysis: an experimental feeding study with large felids. J. Hum. Evol. 80: 114–134.
41. Delaney-Rivera, C., T.W. Plummer, J.A. Hodgson, et al. 2009. Pits and pitfalls: taxonomic variability and patterning in tooth mark dimensions. J. Archaeol. Sci. 36: 2597–2608.
42. Andrés, M., A.O. Gidna, J. Yravedra & M. Domínguez-Rodrigo. 2012. A study of dimensional differences of tooth marks (pits and scores) on bones modified by small and large carnivores. Archael. Anthropol. Sci. 4: 209–219.
43. Parkinson, J.A., T.W. Plummer & R. Bose. 2014. A GIS-based approach to documenting large canid damage to bones. Palaeoecoq. Palaeoecometol. Palaeoecol. 409: 57–71.
44. Galán, A.B., M. Rodríguez, S. de Jauna & M. Domínguez-Rodrigo. 2009. A new experimental study on percussion marks and notches and their bearing on the interpretation of hammerstone-broken faunal assemblages. J. Archaeol. Sci. 36: 776–784.
45. Binford, L.R. 1981. Bones: Ancient Men and Modern Myths. New York: Academic Press.
46. O’Connell, J.F., K. Hawkes, K. Lupo, & N.G. Blarton Jones. 2002. Male strategies and plio-pleistocene archaeology. J. Hum. Evol. 43: 831–872.
47. Domínguez-Rodrigo, M., E. Baquedano, E. Organista, et al. 2021. Early pleistocene faunivorous hominins were not kleptoparasitic, and this impacted the evolution of human anatomy and socio-ecology. Sci. Rep. 11: 16135.
48. Domínguez-Rodrigo, M. & R. Barba. 2007. The behavioral meaning of cut marks at the FLK Zinj level: the carnivore–hominid–carnivore hypothesis falsified (II). In Deconstructing Olduvai: A Taphonomic Study of the Bed I Sites. E. Delson & R.D.E. MacPhee, Eds.: 75–100. Springer Netherlands.
49. Galán, A.B. & M. Domínguez-Rodrigo. 2013. An experimental study of the anatomical distribution of cut marks created by filleting and disarticulation on long bone ends. Archaeometry 55: 1132–1149.
50. Domínguez-Rodrigo, M., A. Gidna, E. Baquedano, et al. 2021. A 3D taphonomic model of long bone modification by lions in medium-sized ungulate carcasses. Sci. Rep. 11: 4944.
51. Potts, R. 1988. Early Hominid Activities at Olduvai. Aldine-Transaction.
52. Marean, C.W. & C. Elehurdt. 1995. Paleoanthropological and paleoecological implications of the taphonomy of a SaberTooth’s Den. J. Hum. Evol. 29: 515–547.
53. O’Connell, J.F., K. Hawkes & N.B. Jones. 1988. Hadza scavenging: implications for plio/pleistocene hominid subsistence. Curr. Anthropol. 29: 356–363.
54. Bunn, H.T., L.E. Bartram & E.M. Kroll. 1988. Variability in bone assemblage formation from Hadza hunting, scavenging, and carcass processing. J. Anthropol. Archaeol. 7: 412–457.
55. Domínguez-Rodrigo, M., J. Yravedra & E. Organista. 2015. A new methodological approach to the taphonomic study of paleontological and archaeological faunal assemblages: a preliminary case study from Olduvai Gorge. J. Archaeol. Sci. 59: 35–53.
56. Schaller, G.B. 2009. The Serengeti Lion: A Study of Predator–Prey Relations. Chicago, IL: University of Chicago Press.