



Geometric-morphometric analysis of tooth pits and the identification of felid and hyenid agency in bone modification

Mari Carmen Arriaza^{a,b,c,*}, Julia Aramendi^{c,d}, Miguel Ángel Maté-González^e, José Yravedra^d, Enrique Baquedano^{c,f}, Diego González-Aguilera^e, Manuel Domínguez-Rodrigo^{c,d,g}

^a School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand, Private Bag 3, 2050, South Africa

^b Centre of Excellence in Palaeosciences, University of the Witwatersrand, Johannesburg, South Africa

^c Institute of Evolution in Africa (IDEA), Covarrubias 36, 28010, Madrid, Spain

^d Department of Prehistory, Complutense University, 28040, Madrid, Spain

^e Superior Polytechnic School of Ávila - University of Salamanca, Department of Cartographic and Terrain Engineering - TIDOP Research Group, Spain

^f Museo Arqueológico Regional, Alcalá de Henares, Madrid, Spain

^g Real Colegio Complutense at Harvard, 26 Trowbridge Street, Cambridge, MA, 02138, USA

ARTICLE INFO

Keywords:

Structured light scanner
Geometric morphometry
Pits
Hyena
Lion
FLK Zinj

ABSTRACT

Carnivore bone modification has been one of the targets of taphonomic research during the last decades. Discerning carnivore involvement in the archaeo-paleontological record during the Plio-Pleistocene is especially important due to the capability of several carnivores of creating bone assemblages, to the interaction with other species in the modification of bones across the landscape and to the potential interspecific competition (e.g., with other carnivores or hominins). Several variables have been explored to discern the carnivore taxa involved in bone modification, but most of them led to equifinality. Recently, the application of computer vision and geometric morphometric techniques for the reconstruction of tooth mark morphology has provided satisfactory results in terms of differentiating among carnivore taxa with similar body size. Here we apply this new technique to the study of pits from the Olduvai Carnivore site (OCS), which has been interpreted as the first bone assemblage generated by lions and subsequently ravaged by hyenas. Results support the lions' involvement and post-ravaging action of hyenas in the OCS assemblage. Lastly, we also explore the potential of applying these new techniques to other bone assemblages in which different carnivore taxa were involved in their modification.

1. Introduction

Hominin-carnivore interactions are a key issue accounted for by taphonomists to better understand the evolution of human behavior. During the Plio-Pleistocene, carnivores have preyed on hominins, have produced bone accumulations or have scavenged remains from archaeological sites (e.g., Brain, 1981; Binford, 1981; Blumenschine, 1986, 1988; Marean, 1991; Marean and Spencer, 1991). Several approaches have been developed to accurately recognize the degree of carnivore involvement in bone modification of the archaeo-paleontological record.

During the earlier stages of neo-taphonomic carnivore research, bone assemblages from carnivore dens created by several species of the savannah ecosystem were described: spotted hyena (*Crocuta crocuta*) (Sutcliffe, 1970; Bearder, 1977; Henschel et al., 1979), striped hyena (*Hyena hyena*) (Kruuk, 1976; Skinner et al., 1980), brown hyena

(*Parahyena brunnea*) (Skinner, 1976; Mills and Mills, 1977; Owens and Owens, 1978) and leopards (*Panthera pardus*) (Brain, 1981; Kerbis-Peterhans, 1990; Ruitter and Berger, 2000). The taphonomic characteristics of these assemblages were described in order to identify if any archaeofaunal assemblage had been accumulated by any of these carnivores. Some classical taphonomic features rely on tooth mark frequencies, skeletal part representation, the age class selection or bone breakage patterns (e.g., Brain, 1981; Binford, 1981; Bunn, 1982; Blumenschine, 1986, 1988). For instance, Cruz-Urbe (1991) suggested six criteria for distinguishing bone assemblages accumulated by hyenas from those accumulated by humans: carnivore-ungulate ratio, tooth frequency, bone breakage, cranial-postcranial ratio, representation of small bones and age classes. Further research conducted by Pickering (2002) showed that only three of these criteria were valid to accurately differentiate bone accumulations produced by hyenas and humans. Carnivores show a great variability as taphonomic agents (e.g., Lam,

* Corresponding author. School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand, Private Bag 3, 2050, South Africa.
E-mail address: maria.arriazadorado@wits.ac.za (M.C. Arriaza).

1992; Egeland et al., 2008; Prendergast and Domínguez-Rodrigo, 2008). Some of their characteristics are constrained by ecological variables (Arriaza et al., 2015). In addition to this, new species have been described as potential accumulating agents, such as nomadic lions as documented in the modern Olduvai Carnivore Site (OCS) (Arriaza et al., 2016). OCS contains a minimum of 55 blue wildebeests (*Connochaetes taurinus*). The study of the skeletal part representation, the low breakage of long bones (higher frequency of Bunn's (1982) circumference type 3 and only 37 notches were documented), the low frequency of tooth marks (only 7% of the sample shows some kind of carnivore damage, including furrowing) and their distribution on long bones, and the modification pattern of the axial skeleton (only 20.7% of these elements show carnivore damage and focused mainly on the apophyses), suggest that a felid was the most likely accumulating agent at OCS. The accumulation rate (426 estimated specimens per year), body mass of the prey (bovid size 3), the specialized-pattern of only one ungulate species, and the topography and environment of the site suggest that the primary accumulating agent was a nomadic lion (Arriaza et al., 2016). Moreover, the low frequency of axial elements, the tooth pit size ranges, the furrowing patterns and the taphotypes documented indicate that the spotted hyena scavenged a substantial part of the bones. Thus, both the lion and the spotted hyaena modified the OCS bone assemblage (Arriaza et al., 2016, 2017). The OCS constitutes the first specialized bone assemblage interpreted as an accumulation performed by a felid that is larger than a leopard. This constitutes a new referential framework for the study of the accumulation of carcasses during the Plio-Pleistocene that should be particularly considered, when the bone assemblage is dominated by medium-sized ungulates and the taxonomic representation shows a specialized profile.

Some studies have focused on the scavenging process conducted by carnivores on bone assemblages primarily consumed by humans (e.g., Brain, 1967, 1969; Blumenschine, 1988; Binford et al., 1988). These experiments on carnivore ravaging bone remains discarded by humans are divided into ethnoarchaeological studies, carnivore kills and taphonomic modelling of human butchery (e.g., Brain, 1969; Blumenschine, 1988; Binford et al., 1988; Domínguez-Rodrigo, 1999; Cleghorn and Marean, 2007). One of the most widely cited study is the seminal experiment carried out by Blumenschine (1988) in the Serengeti National Park using bovid limb bones. A comparison of bone assemblages intensively exploited to obtain marrow by hammerstone breakage only (HO), and hammerstone generated assemblages subsequently scavenged by spotted hyenas (H–C) was carried out (Blumenschine, 1988). Hammerstone generated assemblages secondarily scavenged by spotted hyenas (H–C) were different from those created by hammerstone breakage only (HO), or by spotted hyenas only (CO) (Blumenschine, 1988). Most of the earliest carnivore neotaphonomic research, as the experiments aforementioned, was conducted to address the hunting-scavenging debate among early Pleistocene hominins. The coexistence of cut marks, percussion marks along with tooth marks on bone remains from the FLK Zinj (Olduvai, Tanzania) led to opposite hypotheses about early hominin behaviour (e.g., Leakey, 1971; Binford, 1981; Bunn, 1982; Bunn and Kroll, 1986; Potts, 1988; Blumenschine, 1986, 1988; Domínguez-Rodrigo et al., 2007a, 2014). For the construction and discussion of these hypotheses, several neotaphonomic models were explored. For instance, Selvaggio (1994) developed a carnivore-hominin-carnivore model with several carnivore species. Recently, Pante et al. (2012) extended the model including vultures as the first bone modifier (vulture-hominin-carnivore), following previous experimental work by Domínguez-Solera and Domínguez-Rodrigo (2011). Subsequently, felid-hominin (F–H), felid-hominin-hyena (F–H–H) or hominin-carnivores (H–C) were revisited to be compared with the vulture-hominin-carnivore model and the FLK Zinj assemblage (Domínguez-Rodrigo et al., 2014).

Despite all this effort, further neotaphonomic research on bone surface modifications (BSM) is needed because the experiments and the variables frequently show some biases produced by experimental

sample sizes, the equifinality of some variables, or the challenge of taphonomically studying multi-agent scenarios (e.g., Delaney-Rivera et al., 2009; Domínguez-Rodrigo and Pickering, 2010). New techniques have been applied in neotaphonomy to solve some of these shortcomings, including geometric morphometric and micro-photogrammetric methods. Such techniques have been used for the analysis of cut marks (Maté-González et al., 2015, 2016) and tooth marks (scores), obtaining promising results when differentiating scores produced by different carnivores (Yravedra et al., 2017). This new technique has been applied to the score sample of the OCS to reinforce the “lion-made bone assemblage” interpretation. Results showed that the OCS scores fell in the 95% confidence ellipse corresponding to lions, being 68% of the marks directly associated with the lion ellipse. The 32% remaining scores were grouped differently: 24% appeared associated with hyena scores and 8% lied outside the range of variability described by both carnivores (Arriaza et al., 2017). Thus, this analysis further supported the “lion-made bone assemblage” interpretation of the OCS. Likewise, the analysis of the score morphology also highlighted the hyena involvement in bone modification as a secondary agent (Arriaza et al., 2017).

Recently, the 3D morphometric technique has been applied to pit morphology to assess the feasibility of the method to distinguish between carnivore species based on the study of this type of tooth mark. Results showed that hyena and lion pit morphology can be statistically differentiated (Aramendi et al., 2017a). Given the importance of the new taphonomic framework (lions as bone accumulators), further analysis needs to be conducted to endorse the hypothesis of the involvement of the lion and the spotted hyena in the OCS bone assemblage.

The aim of this paper is the study of the OCS pit morphology through the use 3D virtual models and geometric morphometric techniques. The results obtained here alongside the previous study on score morphology (Arriaza et al., 2017) might shed light upon the involvement of the lion and the spotted hyena in the OCS bone assemblage. The use of this novel technique for the study of carnivore multi-agent scenarios and the implications for early archaeological sites is also explored.

2. Material and methods

2.1. Material

Traditionally, the access order on the consumption process of carcasses by the different kind of carnivores (felids, hyenids, canids) has been tested based on the frequency and the distribution of tooth marks on long bones. The focus on long bones is due to the fact that carnivore taphonomy has been developed primarily on these elements to test hominin-carnivore potential interactions in the formation of prehistoric bone assemblages, which are dominated by these elements (e.g., Blumenschine, 1988; Gidna et al., 2014). For this reason, 19 OCS long bones bearing tooth marks were selected for the present study aiming at differentiating tooth marks inflicted by lions and hyenas, and the access order of both agents. The sample includes 1 femur, 5 humeri, 6 tibiae, 3 radii and 4 metacarpals. For this study, we have only analysed tooth pits, since previous experimental analyses have demonstrated that these tooth marks yielded successful results when differentiating carnivore types (Aramendi et al., 2017a) and the score morphology of the OCS has already been analysed (Arriaza et al., 2017). A total of 28 pits located on shafts were selected on the basis of their optimal preservation. We excluded the rest of pits located on the shaft of long bones: those pits that had bad cortical preservation or some type of alteration, such as the appearance of biochemical modifications or exfoliation. Neither superficial nor inconspicuous tooth marks that provided a bad resolution when photographed stereographically have been selected for the study. Thus, we selected all the pits located on shafts which showed good preservation. Our comparative sample consists of 45 tooth pits on

Table 1
Technical specifications of the Structured Light Scanner SLS-2.

Workpiece size	16 × 500 mm
Resolution	Up to 0.1% of scan size (down to 0.016 mm)
Scanning time	One single scan within a few seconds
Mesh density	Up to 12,000,000 vertices per scan

adult horse long bones generated by spotted hyenas (N 21) and lions (N 24) in a controlled setting, the Cabárceno Nature Park in Cantabria (Northern Spain). The ichnological sample from this experimental sample was derived from experiments conducted with lions, wild dogs and hyenas. For further detail on bone samples used in this work see [Gidna et al. \(2013\)](#), [Domínguez-Rodrigo et al. \(2015\)](#) and [Aramendi et al. \(2017a\)](#).

2.2. Structured light scanner

Tooth marks were digitized with a DAVID structured-light scanner SLS-2 ([Table 1](#)) which was improved with a macro lens that gets better optical resolutions. This equipment is located at the C.A.I. of Archaeometry at the Complutense University (Madrid). The equipment consists of a camera, a projector, and a calibration marker board, which in the first phase, needs to be calibrated. The position and the calibration process were carried out following the criteria summarized in [Maté-González et al. \(2017\)](#). This equipment successfully reproduced most of the tooth pits identified on our experimental samples ([Fig. 1](#)). Inconspicuous marks whose main morphological exterior and interior features could not be appreciated were excluded.

2.3. Geometric morphometrics analysis

Geometric morphometric analyses use information captured in the form of homologous landmarks that describe each specimen independently. For this analysis, pits were described using 17 3D homologous and reliable points that map the exterior and interior surface of the pits as specified in [Aramendi et al. \(2017a\)](#) ([Fig. 1](#)). The landmarking step was performed in Avizo (Visualisation Sciences Group, USA). Landmarks contain shape and size information in the form of Cartesian coordinates, allowing the comparison of the specimens under study ([O'Higgins and Johnson, 1988](#); [Bookstein, 1991](#); [Hall, 2003](#); [Klingenberg, 2008](#)). The technique requires the normalization of the data by superimposition procedures (Procrustes superimposition) that involve the translation, rotation and scaling of shapes defined by

landmark configurations. After the generalized procrustes analysis (GPA), there are always some remaining differences that expose patterns of variation and covariation between structures that after being projected into a flat Euclidian space can be analysed by means of common multivariate statistics ([Richtsmeier et al., 2002](#); [Slice, 2001](#); [Rohlf, 1999](#)).

Geometric morphometric studies also necessitate techniques for dimension reduction since the number of variables tends to be much higher than the number of cases. A commonly used method for simplification that also assesses patterns of variation among the data is principal component analysis (PCA). PCAs were performed in shape and form space to estimate similarities and differences of the OCS, hyena and lions sample on a bidimensional Euclidean space. Form spaces containing size and shape information were obtained by re-scaling data using the natural logarithm of Centroid Size. PCAs were performed in Morphologika 2.5 ([O'Higgins and Jones, 1998](#)). 3D scatter plots of the PCAs were performed in the free software R ([www.rproject.org, Core-Team, 2015](#)) using the `pca3d` library. Differences in shape and form were visualized with the aid of transformation grids ([Bookstein, 1989](#)), computing the extreme changes on the first three PC scores.

Differences between groups were statistically tested to classify the OCS sample. First, multiple variance analyses (MANOVA) on the PC scores were performed in R ([www.rproject.org, Core-Team, 2015](#)) to assess the separation between groups based on their means. Additionally, linear discriminant analyses (LDA) on the shape and form data were performed to determine differences and similarities among groups. LDA provides differences a priori established groups by calculating confusion matrices. In this case three groups were defined: hyenas, lions and OCS. The jack-knife crossvalidated LDA function included in the MASS R package was used.

3. Results

The PCAs of the carnivore sample pits and the OCS pits in shape ([Fig. 2](#)) and form space ([Fig. 3](#)) show a non-polarized morphospace, defined by a high number of PCs. In shape space, the first two PCs explain only 40.6% of the total variance (PC1 = 22.9%, PC2 = 17.7%), while the variance expressed in the scatter-plot in form space is mainly explained by PC1 (85.2%) and PC2 (3.4%).

In the shape space scatter-plot ([Fig. 2](#)), the first PC (22.9%) appears to be related to changes in the interior area of the pit and the overall inclination and shape of the mark. The three groups of pits vary similarly in the direction described by PC1. However, the pits generated by

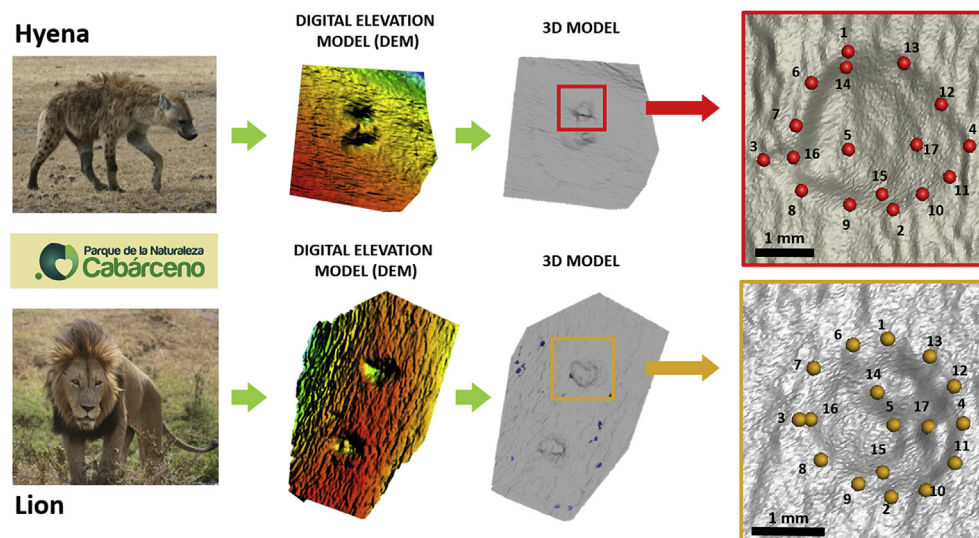


Fig. 1. Digital elevation model of the tooth marks along with the 17 landmarks performed.

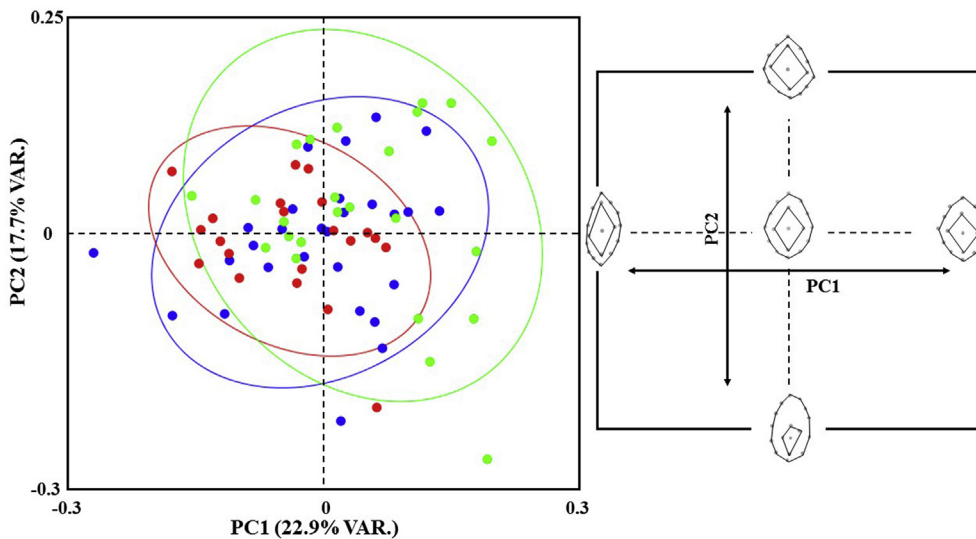


Fig. 2. PCA scatter plot in shape space with confidence ellipses (hyenas: red; lions: green; OCS: blue). The mean shape in the center and the extreme changes in shape along PC1 and PC2 are represented in the schematic version of the graph. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

hyenas show less dispersion than those produced by lions and the ones observed in the OCS. The second PC (17.7%) in shape space is related to the expansion of the interior area and to the location of the widest axis of the pit. In both, PC1 and PC2, changes in the depth of the pits are also remarkable. The pits generated by lions show the widest dispersion along PC2, while hyenas show the lowest scattering range. The OCS sample falls in this case between the ranges described by hyenas and lions.

Shape changes along PC3 (14.5%) were also observed because the first two PCs do not even account for half of the shape variance of the sample. The third PC is characterized by overall morphological differences: elongated versus circular shape (Fig. 4). The dispersion of the hyenas and the OCS sample is similar along PC3, whereas lions seem to be scattered in the opposite direction (Supplementary File 1).

Supplementary video related to this article can be found at <https://doi.org/10.1016/j.quaint.2018.11.023>.

In form space, the overlap between the three groups is still remarkable (Supplementary File 2, Fig. 3). The incorporation of size expands the area occupied by lions and the OCS, especially the former one. On the other side, hyenas tend to be more compressed, but the area outlined by its 95% confidence ellipse fully overlaps with the OCS

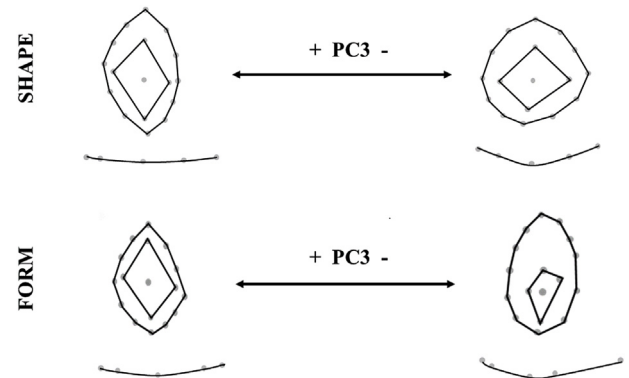


Fig. 4. Extreme shape and form changes represented by the third PC score.

sample and mostly coincides with the ellipse formed by lions; only two hyena pits do not fall in the range described by lions (Supplementary File 2). When the centroid size of the pits is considered (Fig. 3), the variance explained by the first PC increases considerably (85.2%). PC1 is related to changes in the overall form of the pits with wider pits at the

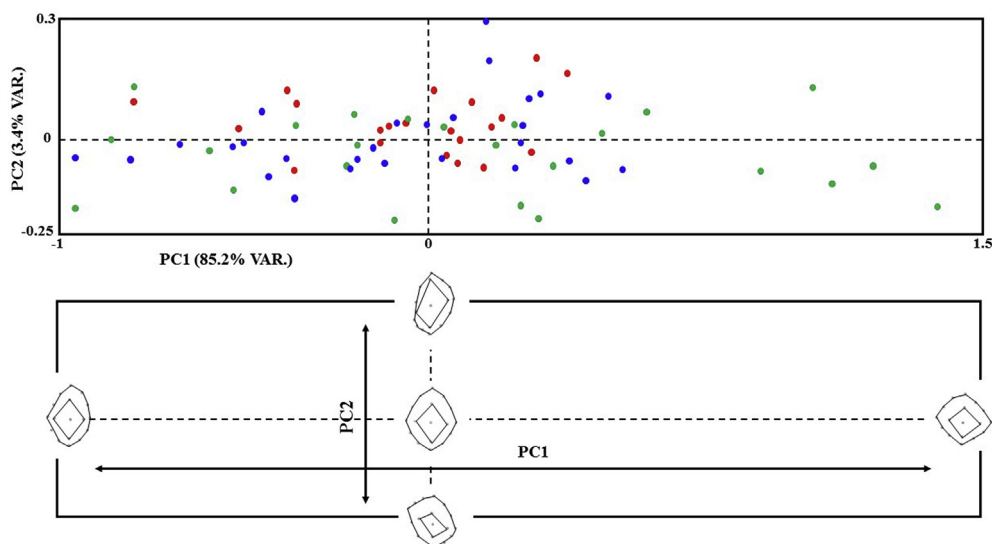


Fig. 3. A) PCA scatter plot in form space (hyenas: red; lions: green; OCS: blue) B) PCA scheme with extreme form changes described by the first two PCs and the average form in the center. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Pairwise MANOVA results.

	Shape space		Form space	
	Hyenas	Lions	Hyenas	Lions
OCS	0.0495	0.4222	0.7564	0.3213
Hyenas		0.0122		0.0563
Lions	0.0122		0.0563	

positive limit of the x-axis and longer and narrower pits at the negative limit of the x-axis. PC2 (3.4%) is characterized by changes in the inclination of the pit and in the size and shape of the interior area of the pit. Form changes expressed by PC3 (Fig. 4) correspond to those expressed by PC2 in shape space (Fig. 2).

Supplementary video related to this article can be found at <https://doi.org/10.1016/j.quaint.2018.11.023>

The similarities and differences observed among the sample scattering in shape and form space were further investigated using several statistical tests. The Pairwise MANOVAs performed on the PC scores to assess the differences among group means show the resemblance of the OCS pits with the lion sample in shape and form (Table 2). Hyenas' pits cannot significantly be distinguished from the OCS when size is considered, but exclusively morphologic features allow the distinction between the two data sets (Table 2). In this study, the sample does not include a wide size variation, indeed only five lion pits appear separated from the main scatter area where the hyena, lion and OCS samples are distributed. Thus, the inclusion of this variable could be tarnishing the pure shape characteristics that distinguish the different carnivore sets. In fact, lions and hyenas can be clearly distinguished considering only shape features ($p = 0.0122$), but cannot be significantly separated when also size is assessed, though the significance level is close to the 0.05 limit ($p = 0.0563$).

The jackknife cross-validated LDA supports these results,

Table 3
Classification of pits using posterior probabilities from cross-validated LDA.

LDA based on shape variables					LDA based on form variables			
Sample	CV	Probability of association			CV	Probability of association		
		Hyena	Lion	OCS		Hyena	Lion	OCS
OCS	Lion	27.6%	36.6%	35.8%	OCS	32.1%	22.8%	45.1%
OCS	OCS	23.8%	30.9%	45.3%	OCS	30.2%	24.4%	45.4%
OCS	OCS	13.1%	40.8%	46.1%	OCS	33.4%	25.0%	41.6%
OCS	OCS	19.0%	31.0%	50.0%	OCS	32.0%	22.4%	45.6%
OCS	Lion	28.0%	48.3%	23.7%	Lion	29.0%	36.7%	34.3%
OCS	OCS	22.5%	30.0%	47.5%	OCS	30.9%	24.5%	44.6%
OCS	Lion	16.0%	63.5%	20.5%	Lion	22.4%	46.0%	31.6%
OCS	Lion	1.2%	54.2%	44.6%	OCS	30.4%	28.8%	40.8%
OCS	Lion	18.9%	48.0%	33.1%	OCS	30.3%	29.0%	40.7%
OCS	Hyena	68.0%	9.0%	23.0%	OCS	41.4%	8.8%	49.8%
OCS	Hyena	46.1%	8.5%	45.4%	Hyena	56.9%	2.2%	40.9%
OCS	OCS	35.6%	20.9%	43.5%	OCS	33.4%	17.1%	49.5%
OCS	Lion	10.3%	61.6%	28.1%	OCS	26.5%	33.4%	40.1%
OCS	OCS	24.9%	21.5%	53.6%	OCS	34.2%	20.1%	45.7%
OCS	Hyena	50.3%	16.6%	33.1%	OCS	32.1%	17.1%	50.8%
OCS	Hyena	35.0%	31.5%	33.5%	OCS	32.3%	24.4%	43.3%
OCS	Lion	8.0%	70.1%	21.9%	Lion	13.9%	60.8%	25.3%
OCS	Lion	17.5%	52.4%	30.1%	Lion	22.6%	44.6%	32.8%
OCS	Lion	14.8%	60.8%	24.4%	Lion	19.2%	64.1%	16.7%
OCS	Hyena	69.2%	5.3%	25.5%	Hyena	47.1%	5.9%	47.0%
OCS	OCS	24.4%	32.1%	43.5%	OCS	32.1%	23.9%	44.0%
OCS	Hyena	52.4%	6.0%	41.6%	Hyena	59.1%	8.9%	32.0%
OCS	Lion	18.0%	54.2%	27.8%	Lion	22.4%	61.6%	16.0%
OCS	OCS	16.3%	39.5%	44.2%	OCS	28.8%	29.3%	41.9%
OCS	Lion	6.8%	59.6%	33.6%	OCS	31.5%	26.9%	41.6%
OCS	Hyena	80.4%	4.6%	15.0%	Hyena	50.3%	14.4%	35.3%
OCS	OCS	14.8%	25.0%	60.2%	OCS	32.1%	22.8%	45.1%
OCS	OCS	19.3%	14.5%	66.2%	OCS	32.4%	13.8%	53.8%

highlighting the similarities between the OCS and the lion sample when pure shape variables are considered (Table 3). The confusion matrix calculated indicates that OCS pits are mainly undistinguishable from those generated by lions ($n = 11$), whereas only 7 pits of 28 cannot be distinguished from the hyena sample. The remaining OCS pits ($n = 10$) cannot be classified neither as lion nor as hyena. Though many OCS pits cannot be assigned to any of the carnivores, it can be noticed that among those 10 unclassified OCS pits, 7 pits would more likely be assigned to lions than to hyenas. These misclassification rates increase when the analysis is performed on form data (Table 3). In this case, only 6 OCS pits are classified as lion and 4 are considered hyena. The majority of the OCS sample ($n = 18$) cannot be assigned to any of the groups, and according to the association probabilities calculated by the LDA most unclassified OCS pits would rather be associated with the action of hyenas than to lions.

However, all the unclassified OCS pits show percentages that do not reach the 50%, except in one case, whereas OCS pits classified as lions or hyenas are usually supported by higher association probabilities. The confusion generated by the similarity of the whole pit sample is significant and is in line with previous taphonomic and morphometric analyses that identified the action of both carnivores at the site. Likewise, it should be borne in mind that pits produced by hyenas and lions can easily be confused generating higher misclassification rates, as already shown in Aramendi et al. (2017a).

4. Discussion

One of the greatest taphonomic challenges to the interpretation of archaeological bone assemblages is that most of them are palimpsests. This means that several processes intervened during the formation of the archaeological record. A great effort has been made to clarify the taphonomic signals left by the different processes involved in a multi-agent scenario. For instance, the taphonomic analysis of the FLK Zinj bone assemblage showed the presence of cut marks along with tooth

marks carried out by carnivores (e.g., Bunn, 1982; Bunn and Kroll, 1986; Potts and Shipman, 1981; Shipman, 1986). This inspired several neotaphonomic experiments in order to clarify the access order of hominins and carnivores in a multi-agent scenario: hammerstone only model (HO) and carnivore only (CO) (Blumenshine, 1988, 1995), carnivore-hominin-carnivore (C–H–C) (Selvaggio, 1994), hammerstone to carnivore (H–C) (Capaldo, 1995), vulture-hominin-carnivore (V–H–C) (Pante et al., 2012) or felid-hominin (F–H), felid-hominin-hyena (F–H–H) and hominin-carnivore (H–C) models (Domínguez-Rodrigo et al., 2014).

In addition to the concern raised by the multi-patterned scenario, some taphonomic variables show equifinality. For example, skeletal part representation has been used to determine the accumulating agent based on the specific manner of transporting and accumulating carried out by humans and non-anthropogenic agents (i.e., carnivores). For instance, the skeletal profiles of FLK Zinj, biased towards long limb bones, provided supporting arguments for both hypotheses (e.g., Binford, 1981, Binford et al., 1988; Bunn and Kroll, 1986, 1988; Potts, 1988; Blumenshine et al., 1996). Based on modern ethnographic analogs, skeletal part representation of the FLK Zinj was interpreted as a key indicator of primary anthropogenic access to carcasses and body part selective transportation (e.g., Bunn and Kroll, 1986, 1988). Using the same profiles, Binford (1981) argued that carcasses could have been initially accumulated by carnivores at sites and secondarily accessed by humans. A third hypothesis stated that humans scavenged at carnivore kills and transported carcasses to sites (Blumenshine, 1986, 1995; Capaldo, 1995; Selvaggio, 1994). Recently, new methods based on multivariate statistics have been proposed for the analysis of classical taphonomic features such as the skeletal part representation or cut marks. For instance, the use of machine learning methods allows the distinction of skeletal part representations generated by felids from those documented in hyena dens (Arriaza and Domínguez-Rodrigo, 2016), and marks generated by different agents can be discerned (Egeland et al., 2018, Domínguez-Rodrigo and Baquedano, 2018). Thus, machine learning methods overcome the equifinality problems caused by skeletal part representation. With this in mind, neotaphonomic research must focus on elaborating accurate analogues to reproduce the multi-agent scenario avoiding equifinality. The present analysis could contribute to this debate by analysing tooth mark morphology on said assemblages providing evidence of felid or hyenid bone modification, thus further supporting interpretive scenarios characterized by hominin primary or secondary action.

Carnivores have been the main focus of neotaphonomic research during the last decades. Carnivores may be considered potential accumulating agents; they might have scavenged bone remains from archaeological sites and they might have preyed on hominins during the Plio-Pleistocene (e.g., Sutcliffe, 1970; Brain, 1981; Blumenshine, 1988). Some of the variables used to determine the carnivore species involved in bone modification also show equifinality problems, e.g., tooth mark dimension. This variable has been used to discuss the bone assemblage from the FLK Zinj (Selvaggio, 1994; Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003). The mean tooth pit size on cancellous bone from the FLK Zinj was similar to the pit size observed in a modern sample consumed by hyenas and lions (Selvaggio and Wilder, 2001). However, the results on the cortical bone (i.e. shafts) suggested that the sample from the FLK Zinj was similar to modern samples generated by cheetah, leopard or hyenas (Selvaggio and Wilder, 2001). Based on these data, Selvaggio and Wilder (2001) stated that hyenas were the last modifying agent on the FLK Zinj bone assemblage. Either hyenas were ravaging carcasses left by hominins, or felids firstly defleshed the carcasses, followed by hominins demarrowing them and hyenas ravaging the abandoned bones (Selvaggio and Wilder, 2001). Further research analysed the same carnivore taxa revealing that tooth mark size also reached equifinality (Domínguez-Rodrigo and Piqueras, 2003). Several species showed overlapping pit sizes. On the other hand, according to this study it was possible to differentiate between small-

medium carnivores and larger species based on tooth mark sizes on both cancellous and cortical bone sections (Domínguez-Rodrigo and Piqueras, 2003). The great variability suggested by tooth mark size analysis could not support the three-stage model hypothesis (felid-hominin-hyenid) for the FLK Zinj. Subsequently, other taxa (carnivorous and omnivorous) were studied, such as the tiger, bobcat or caracal (Delaney-Rivera et al., 2009) and the sample size of carnivores species previously studied was increased (Andres et al., 2012). The body mass of the taxa and the bone portion where the tooth mark was inflicted may determine the tooth mark dimensions (Selvaggio, 1994; Delaney-Rivera et al., 2009). Indeed, despite some overlapping, small and large carnivores could be differentiated based on the tooth pits inflicted on cortical bone (shafts) (Delaney-Rivera et al., 2009; Andres et al., 2012). Nevertheless, this variable alone was not a good indicator of the carnivore species involved in the exploitation of carcasses. By virtue of the importance of hominin-carnivore interactions, we should continuously improve the neotaphonomic frameworks and techniques to develop accurate analogs to compare with archaeological sites.

One of the recent contributions to the understanding of carnivore neotaphonomy has been launched by the description of the first lion-made bone assemblage (Arriaza et al., 2016). Until then, the only felid that had been interpreted as a potential accumulating agent was the leopard (e.g., Brain, 1981; Ruitter and Berger, 2000). Hence, any bone assemblage including larger prey sizes than the usually hunted by leopards may not be related to the action of a felid. However, large felids had been proposed as the primary accumulating agent at some palaeoanthropological sites, such as FLK N, FLK NN, DK and AMK at Olduvai Gorge (Domínguez-Rodrigo et al., 2007a,b; Aramendi et al., 2017b) or the fossil *Bovidae* assemblage from Sterkfontein (South Africa) Member 4 (Vrba, 1976). Nevertheless, these interpretations lacked a modern proxy. It is why the description of the first lion-made bone assemblage is important for the understanding of these relevant palaeoanthropological sites. Several classical taphonomic variables like the skeletal part representation, breakage patterns and tooth mark frequency were used to determine the primary accumulating agent at the OCS. In addition, the most innovative methods to discern carnivore bone modification as the taphotypes (Domínguez-Rodrigo et al., 2015) and the microphotogrammetric reconstruction of scores supported the hypothesis of the lion-made bone assemblage (Arriaza et al., 2016, 2017). Considering that the OCS constitutes a new taphonomic framework, further research was needed to reinforce the hypothesis that large felids produce bone accumulations. Recently, the 3D reconstructions of pits generated by different carnivores have produced successful results concerning the distinction of carnivore species based on the traces they leave on limb bone shafts (Aramendi et al., 2017a). The tooth pit morphology generated by lions and hyenas showed statistical differences (Aramendi et al., 2017a). The application of this method to the OCS shows that pits from the OCS cannot be distinguished from pits generated by lions. On the other hand, pits generated by lions and hyenas as well as pits from the OCS and those produced by hyenas can be statistically distinguished. Thus, pit morphology from the OCS supports the hypothesis of the “lion-made bone assemblage”. Moreover, the analysis comparing the pit morphology produced by hyenas and the OCS, though not significant, is approaching the threshold for statistical significance. This may be due to the secondary access of hyenas to the bone assemblage of the den as suggested by other variables such as the taphotypes (Arriaza et al., 2016) or the microphotogrammetric analysis of scores (Arriaza et al., 2017). The morphometric analysis showed that the OCS scores grouped into the ellipse corresponding to the lions, being 68% of the marks directly associated with the lion ellipse. The 32% remaining scores were scattered differently: 24% appeared associated with hyena scores and 8% lied outside the range of variability described by both carnivores (Arriaza et al., 2017). The results obtained from the morphometric analysis of scores suggest that hyenas accessed the OCS bone assemblage secondarily. In contrast, although the similarity between the OCS pit morphology and the hyena sample is not

significant, the statistic correlation is close to the significance level (Table 2). The confusion matrix calculated indicates that OCS pits are mainly confused with those generated by lions ($n = 11$), whereas only 7 pits of 28 cannot be distinguished from the hyena sample. The remaining OCS pits ($n = 10$) cannot be classified neither as lion nor as hyena. In sum, around 40% of the OCS pits match those generated by lions, while only 25% of the OCS pits match hyenas' pits. Thus, the application of the same technique (3D reconstructions) on different type of tooth marks (pit vs scores) may vary slightly the taphonomic interpretation. This may be due to the differences in tooth mark frequency depending on the carnivore. Durophagous carnivores (hyenas) are more prone to continuously modify bone surfaces by applying pressure to break bones and, hence, create a higher frequency of tooth pits than strictly flesh-eating carnivores (lions), which would create more scoring while strictly removing flesh (Domínguez-Rodrigo et al., 2012). In experiments carried out with different carnivore species, lions showed a proportion of tooth scores on shafts $> 70\%$, whereas among hyenas (scores = 44%) and wolves (scores = 49%) tooth pits are dominant (Domínguez-Rodrigo et al., 2012). Lion samples include more complete bones with a higher score to pit ratio than hyenas and wolves (Domínguez-Rodrigo et al., 2012). In light of the results presented here, the virtual analysis of tooth marks may differentiate tooth marks carried out by different species, in contrast to previous analyses based on the dimension of tooth marks that hindered the distinction between carnivore species with similar body mass (e.g., lions and hyenas) (Domínguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009; Andres et al., 2012). Thus, the virtual morphometric analysis offers an alternative to deal with the problem of equifinality in the study of tooth mark differentiation. As mentioned earlier, neotaphonomic techniques may also be worthwhile in multi-agent scenarios. The application of this new method to the OCS bone assemblage has given the opportunity to test the new technique in a bone assemblage that bears tooth marks generated by several carnivores (lions and hyenas). When a multi-agent model is analysed with this technique it should be taken into account that the type of tooth mark analysed (pit vs score) may slightly vary the statistical result. If a lion-to-hyena model is tested (as in the case of the OCS), the morphometric analysis of scores may show more accurately the access order of carnivores than the analysis of pits.

The OCS is a relevant bone accumulation since it is the first documented bone assemblage generated by large felids. This interpretation is important for the understanding of archaeological sites like FLK N, FLK NN, DK and AMK (Domínguez-Rodrigo et al., 2007a,b; Aramendi et al., 2017a) at Olduvai Gorge, or the fossil *Bovidae* from Sterkfontein Member 4 (Vrba, 1976). On the other hand, the OCS shows a lion-to-hyena model that took place naturally. This is especially important for the application of this new technique to archaeological bone assemblages. One of the classic hypotheses for the interpretation of the FLK Zinj site relies on the action of hominins as passive scavengers of felid kills and hyenas as marginal agents in the bone modification process (e.g., Cavallo and Blumenschine, 1989; Blumenschine, 1988, 1995; Selvaggio, 1994; Capaldo, 1997). The possible application of this new technique to the FLK Zinj assemblage could shed light on the hunting-vs-scavenging debate raised around the site. Taking into account the results of the present work, the virtual reconstruction of scores and pits from an assemblage modified by large felids and hyenas might be valid to determine the modifying agent as well as to clarify the order of access to the carcasses. If both kind of tooth marks (pits and scores) were mainly produced by a hyena this would indicate only one stage of carnivore bone modification. In contrast, if scores are produced by lions (or lions and secondarily hyenids), this might suggest a lion-to-hyena model. However, the application of this method to the FLK Zinj assemblage still requires the inclusion of leopard tooth mark morphology (work in progress). The 3D virtual reconstruction of tooth marks from the FLK Zinj assemblage could help clarify the taxon/taxa involved in its modification and further hypotheses concerning hominin behaviour could be assessed at the site.

5. Conclusions

The application of computer vision and geometric morphometric techniques in the study of tooth marks has provided the possibility of successfully distinguishing different carnivore taxa involved in bone modification. Variables previously explored such as the dimension of tooth marks are affected by equifinality problems: carnivore taxa with similar body mass generate pits with similar dimensions (e.g., Domínguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009; Andres et al., 2012). The capacity to determine the carnivore taxa involved in bone modifications will improve the understanding of site formation processes and more importantly, of archaeological sites which show both anthropic and carnivore bone modification and the access order of agents is controversial. In this manner, hypotheses regarding hominin subsistence patterns can be explored. The application of this new technique to long bones of the OCS has shown that this methodology is also valid for multi-agent scenarios where several carnivore modifying agents are present. This is especially important for the application of the methodology described here to archaeo-paleontological sites considered palimpsests. The results support that the OCS bone assemblage was first modified by the lion and secondarily ravaged by hyenas.

Acknowledgements

We wish to thank The Ngorongoro Conservation Area Authorities, COSTECH and the Antiquities unit for permits to conduct research at Olduvai. We would like to express our appreciation and acknowledgement to: Julius Sulley, Lazaro Sarwatt, Yacob Matle, Yona Thomas, Thomas Madangi, Nicolaus Dohho, Caroli Maole, Francis Fabiano, Sangau Letuma, Nicodemus Burra, Ibrahim Mathias, Shabany Bakari. The authors greatly appreciate the major funding provided by the Spanish Ministry of Science and Innovation through the European project I + D HAR2013-45246-C3-1P and the Spanish Ministry of Culture through the Heritage Institute and the Program of Funding for Archaeological Projects Abroad. The support of the DST-NRF Centre of Excellence in Palaeosciences (CoE-Pal) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the CoE. And finally we want to recognize the technical support provided by C.A.I. Arqueometry and Archaeological Analysis from Complutense University which has been very useful to carry out the present work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quaint.2018.11.023>.

References

- Andrés, M., Gidna, A., Yravedra, J., Domínguez-Rodrigo, M., 2012. A study of dimensional differences of tooth marks (pits and scores) on bones modified by small and large carnivores. *Archaeol. Anthropol. Sci.* 4, 209–219.
- Aramendi, J., Uribelarra, D., Arriaza, M.C., Arráiz, H., Barboni, D., Yravedra, J., Ortega, M.C., Gidna, A., Mabulla, A., Baquedano, E., Domínguez-Rodrigo, M., 2017b. The paleoecology and taphonomy of AMK (Bed I, Olduvai Gorge) and its contributions to the understanding of the “Zinj” paleolandscape. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 488, 35–49.
- Aramendi, J., Maté-González, M.Á., Yravedra, J., Ortega, M.C., Arriaza, M.C., González-Aguilera, D., Baquedano, E., Domínguez-Rodrigo, M., 2017a. Discerning carnivore agency through the three-dimensional study of tooth pits: revisiting crocodile feeding behaviour at FLK-Zinj and FLK NN3 (Olduvai Gorge, Tanzania). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 488, 93–102.
- Arriaza, M.C., Domínguez-Rodrigo, M., 2016. When felids and hominins ruled at Olduvai Gorge: a machine learning analysis of the skeletal profiles of the non-anthropogenic Bed I sites. *Quat. Sci. Rev.* 139, 43–52.
- Arriaza, M.C., Domínguez-Rodrigo, M., Martínez-Maza, C., Mabulla, A., Baquedano, E., 2015. Differential predation by age and sex classes in blue wildebeest in Serengeti: study of a modern carnivore den in Olduvai Gorge (Tanzania). *PLoS One* 10 (5), e0125944.

- Arriaza, M.C., Domínguez-Rodrigo, M., Yravedra, J., Baquedano, E., 2016. Lions as bone accumulators? Paleontological and ecological implications of a modern bone assemblage from Olduvai Gorge. *PLoS One* 11 (5), e0153797.
- Arriaza, M.C., Yravedra, J., Domínguez-Rodrigo, M., Maté-González, M.Á., García Vargas, E., Palomeque-González, J.F., Aramendi, J., González-Aguilera, D., Baquedano, E., 2017. On applications of micro-photogrammetry and geometric morphometrics to studies of tooth mark morphology: the modern Olduvai Carnivore Site (Tanzania). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 488, 103–112.
- Bearder, S.K., 1977. Feeding habits of spotted hyaenas in a woodland habitat. *East Afr. Wildl. J.* 15, 263–280.
- Binford, L.R., 1981. *Bones Ancient Men and Modern Myths*. New York Academic Press, New York.
- Binford, L.R., Mills, L.G.L., Stone, N.M., 1988. Hyena scavenging behavior and its implications for the interpretation of faunal assemblages from FLK 22 (the Zinj floor) at Olduvai Gorge. *J. Anthropol. Archaeol.* 7, 99–135.
- Blumenschine, R.J., 1986. Early Hominid Scavenging Opportunities. Implications of Carcass Availability in the Serengeti and Ngorongoro Ecosystems. B.A.R. International Series, 283, Oxford.
- Blumenschine, R.J., 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *J. Archaeol. Sci.* 15, 483–502.
- Blumenschine, R.J., 1995. Percussion marks, tooth marks and the 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.
- Blumenschine, R.J., Marean, C.W., Capaldo, S.D., 1996. Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. *J. Archaeol. Sci.* 23, 493–507.
- Bookstein, F., 1989. Principal warps: thin-plate spline and the decomposition of deformations. *Trans. Pattern Anal. Mach. Intell.* 11 (6), 567–585.
- Bookstein, F.L., 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge University Press, New York.
- Brain, C.K., 1967. Hottentot food remains and their bearing on the interpretation of fossil bone assemblages. *Sci. Paper Namib Desert Res. Station* 32, 1–11.
- Brain, C.K., 1969. The contribution of Namib Desert Hottentots to an understanding of *Australopithecine* bone accumulations. *Sci. Paper Namib Desert Res. Station* 39, 13–22.
- Brain, C.K., 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. Chicago University Press, Chicago.
- Bunn, H.T., 1982. Meat-eating and Human Evolution: Studies on the Diet and Subsistence Patterns of Plio-pleistocene Hominids in East Africa. Ph.D. Dissertation. University of California, Berkeley.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by plio-pleistocene hominids at Olduvai Gorge, Tanzania. *Curr. Anthropol.* 27, 431–452.
- Capaldo, S.D., 1995. *Inferring Hominid and Carnivore Behavior from Dual-patterned Archaeofaunal Assemblages*. Ph.D. Dissertation. Rutgers University, New Brunswick.
- Capaldo, S.D., 1997. Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (Zinjanthropus), Olduvai Gorge, Tanzania. *J. Hum. Evol.* 33, 555–597.
- Cavallo, J.A., Blumenschine, R.J., 1989. Tree-stored leopard kills: expanding the hominid scavenging niche. *J. Hum. Evol.* 18, 393–399.
- Cleghorn, N., Marean, C.W., 2007. The destruction of skeletal elements by carnivores: the growth of a general model for skeletal element destruction and survival in zooarchaeological assemblages. In: Pickering, T.R., Schick, K., Toth, N. (Eds.), *Breathing Life into Fossils: Taphonomic Studies in Honor of C.K. (Bob) Brain*. Stone Age Institute Press, Bloomington, pp. 38–66.
- Core-Team, R., 2015. *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.Rproject.org/>.
- Cruz-Urbe, K., 1991. Distinguishing hyaena from hominid bone accumulations. *J. Field Archaeol.* 18, 467–486.
- Delaney-Rivera, C., Plummer, T.W., Hodgson, J.A., Forrest, F., Hertel, F., Oliver, J.S., 2009. Pits and pitfalls: taxonomic variability and patterning in tooth mark dimensions. *J. Archaeol. Sci.* 36, 2597–2608.
- Domínguez-Rodrigo, M., 1999. Flesh availability and bone modification in carcasses consumed by lions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 149, 373–388.
- Domínguez-Rodrigo, M., Baquedano, E., 2018. Distinguishing butchery cut marks from crocodile bite marks through machine learning methods. *Sci. Rep.* 8 (1), 5786.
- Domínguez-Rodrigo, M., Pickering, T.R., 2010. Un estudio tafonómico multivariante de las acumulaciones de fauna de hienidos (*Crocota crocuta*) y félidos (*Panthera pardus*). *Zona Arqueológica* 13, 50–66.
- Domínguez-Rodrigo, M., Piqueras, A., 2003. The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. *J. Archaeol. Sci.* 30, 1385–1391.
- Domínguez-Rodrigo, M., Barba, R., Egeland, C.P., 2007a. Deconstructing Olduvai. A Taphonomic Study of the Bed I Sites. Springer Books, Dordrecht, The Netherlands.
- Domínguez-Rodrigo, M., Egeland, C.P., Pickering, T.R., 2007b. Equifinality in carnivore tooth marks and the extended concept of archaeological palimpsests: implications for models of passive scavenging by hominids. In: Pickering, T.R., Schick, K., Toth, N. (Eds.), *Breathing Life into Fossils: Taphonomic Studies in Honor of C.K. (Bob) Brain*. Stone Age Institute Press, Bloomington, pp. 255–267.
- Domínguez-Rodrigo, M., Gidna, A., Yravedra, J., Musiba, C., 2012. A comparative neotaphonomic study of felids, hyenids and canids: an analogical framework based on long bone modification patterns. *J. Taphonomy* 10, 147–164.
- Domínguez-Rodrigo, M., Bunn, H.T., Yravedra, J., 2014. A critical re-evaluation of bone surface modification models for inferring fossil hominid and carnivore interactions through a multivariate approach: application to the FLK Zinj archaeofaunal assemblage (Olduvai Gorge, Tanzania). *Quat. Int.* 322 (323), 32–43.
- Domínguez-Rodrigo, M., Yravedra, J., Organista, E., Gidna, A., Fourvel, J.P., Baquedano, E., 2015. A new methodological approach to the taphonomic study of paleontological and archaeological faunal assemblages: a preliminary case study from Olduvai Gorge (Tanzania). *J. Archaeol. Sci.* 59, 35–53.
- Domínguez-Solera, S., Domínguez-Rodrigo, M., 2011. A taphonomic study of a carcass consumed by griffon vultures (*Gyps fulvus*) and its relevance for the interpretation of bone surface modifications. *Archaeol. Anthropol. Sci.* 3, 385–392.
- Egeland, A., Egeland, C.P., Bunn, H.T., 2008. Taphonomic analysis of a modern spotted hyena (*Crocota crocuta*) den from Nairobi, Kenya. *J. Taphonomy* 6, 275–299.
- Egeland, C.P., Domínguez-Rodrigo, M., Pickering, T.R., Menter, C.G., Heaton, J.L., 2018. Hominin skeletal part abundances and claims of deliberate disposal of corpses in the Middle Pleistocene. *Proc. Natl. Acad. Sci. Unit. States Am.* 115 (18), 201718678.
- Gidna, A., Yravedra, J., Domínguez-Rodrigo, M., 2013. A cautionary note on the use of captive carnivores to model wild predator behavior: a comparison of long bone modification patterns by lions. *J. Archaeol. Sci.* 40, 1903–1910.
- Gidna, A.O., Kisui, B., Musiba Mabulla, A., Domínguez-Rodrigo, M., 2014. An ecological neo-taphonomic study of carcass consumption by lions in Tarangire National Park (Tanzania) and its evidence for human evolutionary biology. *Quat. Int.* 322 (323), 167–180.
- Hall, B.K., 2003. Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. *Biol. Rev.* 78, 409–433.
- Henschel, J.R., Tilson, R., Von Blottnitz, F., 1979. Implications of a spotted hyena bone assemblage in the Namib Desert. *S. Afr. Archaeol. Bull.* 34, 127–131.
- Kerbis-Peterhans, J.C., 1990. *The Role of Porcupines, Leopards and Hyenas in Ungulate Carcass Dispersal: Implications for Paleoanthropology*. Ph.D. Dissertation. University of Chicago, Chicago.
- Klingenberg, C.P., 2008. Novelty and “Homology-free” morphometrics: what’s in a name? *Evol. Biol.* 35, 186–190.
- Kruuk, H., 1976. Feeding and social behaviour of the striped hyaena (*Hyaena vulgaris* Desmaret). *East Afr. Wildl. J.* 14, 91–111.
- Lam, Y.M., 1992. Variability in the behaviour of spotted hyenas as taphonomic agents. *J. Archaeol. Sci.* 19, 389–406.
- Leakey, M., 1971. Olduvai Gorge. In: *Excavations in Bed I and II, vol. 3*. Cambridge University Press, Cambridge, pp. 1960–1963.
- Marean, C.W., 1991. Measuring the post-depositional destruction of bone archaeological assemblages. *J. Archaeol. Sci.* 18, 677–694.
- Marean, C.W., Spencer, L.M., 1991. Impact of carnivore ravaging on zooarchaeological measures of element abundance. *Am. Antiqu.* 56, 645–658.
- Maté-González, M.Á., Yravedra, J., González-Aguilera, D., Palomeque-González, J.F., Domínguez-Rodrigo, M., 2015. Micro-photogrammetric characterization of cut marks on bones. *J. Archaeol. Sci.* 62, 128–142.
- Maté-González, M.Á., Palomeque-González, J.F., Yravedra, J., González-Aguilera, D., Domínguez-Rodrigo, M., 2016. Micro-photogrammetric and morphometric differentiation of cut marks on bones using metal knives, quartzite and flint flakes. *Archaeol. Anthropol. Sci.* <https://doi.org/10.1007/s12520-016-0401-5>.
- Maté-González, M.Á., Aramendi, J., González-Aguilera, D., Yravedra, J., 2017. Statistical comparison between low-cost methods for 3D characterization of cut-marks on bones. *Rem. Sens.* 9 (9), 873.
- Mills, M.G.L., Mills, M.E.J., 1977. An analysis of bones collected at hyaena breeding dens in the Gemsbok national Parks (*Mammalia: carnivora*). *Ann. Transvaal Mus.* 30 (14), 145–155.
- O’Higgins, P., Johnson, D.R., 1988. The quantitative description and comparison of biological forms. *Crit. Rev. Anat. Sci.* 1, 149–170.
- O’Higgins, P., Jones, N., 1998. Facial growth in *Cercopithecus torquatus*: an application of three dimensional geometric morphometric techniques to the study of morphological variation. *J. Anat.* 193, 251–272.
- Owens, D.D., Owens, M.J., 1978. Feeding ecology and its influence on social organisation in brown hyenas (*Hyaena brunnea*) of the central Kalahari desert. *East Afr. Wildl. J.* 16, 113–136.
- Pante, M.C., Blumenschine, R.J., Capaldo, S.D., Scott, R.S., 2012. Validation of bone surface modification models for inferring fossil hominid and carnivore feeding interactions, with reapplication to FLK 22, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 63 (2), 395–407.
- Pickering, T., 2002. Reconsideration of criteria for differentiating faunal assemblages accumulated by hyenas and hominids. *Int. J. Osteoarchaeol.* 12, 127–141.
- Potts, R., 1988. *Early Hominid Activities at Olduvai*. Aldine, New York.
- Potts, R., Shipman, P., 1981. Cutmarks made by stone tools from Olduvai Gorge, Tanzania. *Nature* 291, 577–580.
- Prendergast, M., Domínguez-Rodrigo, M., 2008. Taphonomic analyses of a hyena den and a natural-death assemblage near Lake Eyasi (Tanzania). *J. Taphonomy* 6, 301–335.
- Richtsmeyer, J.T., DeLeon, V.B., Lele, S.R., 2002. The promise of geometric morphometrics. *Am. J. Phys. Anthropol.* 45, 63–91.
- Rohlf, F.J., 1999. Shape statistics: procrustes superimpositions and tangent spaces. *J. Classif.* 16, 197–223.
- Ruiter, D., Berger, L., 2000. Leopards as taphonomic agents in dolomitic caves—implications for Bone accumulations in the hominid-bearing deposits of South Africa. *J. Archaeol. Sci.* 27, 665–684.
- Selvaggio, M.M., 1994. *Selvaggio MM. Identifying the Timing and Sequence of Hominid and Carnivore Involvement with Plio-pleistocene Bone Assemblages from Carnivore Tooth Marks and Stone Tool Butchery Marks on Bone Surfaces*. Ph.D. Dissertation. Rutgers University, New Brunswick.
- Selvaggio, M.M., Wilder, J., 2001. Identifying the involvement of multiple carnivore taxon with archaeological bone assemblages. *J. Archaeol. Sci.* 28, 465–470.
- Shipman, P., 1986. Scavenging or hunting in early hominids: theoretical framework and tests. *Am. Anthropol.* 88, 27–43.
- Skinner, J.D., 1976. Ecology of the brown hyaena *Hyaena brunnea* in the Transvaal with a

- distribution map for southern Africa. S. Afr. J. Wildl. Res. 72, 262–269.
- Skinner, J.D., Davis, S., Ilani, G., 1980. Bone collecting by striped hyaenas, *Hyaena hyaena*, in Israel. Paleontol. Afric. 23, 99–104.
- Slice, D.E., 2001. Landmark coordinates aligned by procrustes analysis do not lie in Kendall's shape space. Syst. Biol. 50 (1), 141–149.
- Sutcliffe, A.J., 1970. Spotted hyaena: crusher, gnawer, digester and collector of bones. Nature 227 (5263), 1110–1113.
- Vrba, E.S., 1976. The Fossil Bovidae of Sterkfontein, Swartkrans, and Kromdraai. Transvaal Museum, Pretoria, Transvaal Museum Memoir, pp. 21.
- Yravedra, J., García-Vargas, E., Maté-González, M.Á., Aramendi, J., Palomeque-González, J.F., Vallés-Iriso, J., Matesanz-Vicente, J., González-Aguilera, D., Domínguez-Rodrigo, M., 2017. The use of Micro-Photogrammetry and Geometric Morphometrics for identifying carnivore agency in bone assemblages. J. Archaeol. Sci.: Report 14, 106–115.