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ARTICLE



## Characterising leopard as taphonomic agent through the use of micro-photogrammetric reconstruction of tooth marks and pit to score ratio

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### ABSTRACT

Leopards have been the focus of taphonomic research due to their capacity to create bone accumulations, prey on some hominin groups or potentially provide scavenging opportunities to early hominins. Some of the variables explored to characterise felids as taphonomic agents have presented problems of equifinality, such as the frequency of tooth marks on long bone shafts or the dimensions of tooth pits and scores. Recently, new methodologies based on microphotogrammetry and geometric morphometrics have been developed for the morphologic analysis of taphonomic marks, such as tooth marks. Through a review of Bob Brain's neotaphonomic collection, the present study applies these new techniques to reconstruct leopard tooth marks and compare these with tooth marks from lions and spotted hyenas. Along with this, the ratio pit to score, a taphonomic variable previously characterised in lions and spotted hyenas, has been analysed. Results show that tooth marks inflicted by leopards, spotted hyenas and lions can be statistically differentiated based on their morphology. On the other hand, the ratio pit to score inflicted by the leopard is closer to hyenas.

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Neotaphonomy; carnivores; early hominins; geometric morphometrics; landmarks

### Introduction

Since the 19th century, studies aiming to discern carnivore involvement in bone assemblages have generated large attention. Initially, bone assemblages from Wookey Hole Caves (England), among other archeological sites, were interpreted as carnivore accumulations based on actualistic data (Thirria 1833; Tournal 1833; Dawkins 1863, 1874). Currently it is known that several African carnivore species are bone collectors, for example the spotted hyena (*Crocuta crocuta*) (Sutcliffe 1970; Bearder 1977; Henschel et al. 1979), the striped hyena (*Hyaena hyaena*) (Kruuk 1976; Skinner et al. 1980), the brown hyena (*Parahyaena brunnea*) (Skinner 1976; Mills and Mills 1977; Owens and Owens 1978) and the leopard (*Panthera pardus*) (Simons 1966; Brain 1981; Ruitter and Berger 2000). This capacity to create bone accumulations has led to carnivores being considered bone-accumulating agents of the archeo-paleontological record. Carnivores may also interact with other species in the same ecosystem (e.g. other carnivore species or hominins) by scavenging prey hunted by other taxa or by competing for the same resources. For this reason, prey range, age-class selection or carnivore post-ravaging behaviour during the scavenging process, has been intensively explored over the last 40 years (e.g. Kruuk 1972; Schaller 1972; Binford 1981; Brain 1981; Hill 1983; Blumenschine 1986, 1988; Marean and Spencer 1991; Marean et al. 1992). Through the study of these processes, the primary accumulating agent of the archeo-paleontological record can be

explored and further interactions with other predator taxa (e.g. other carnivore species or hominins) can be elucidated.

Since the 1970's and intensively during the 1980's, prolific neotaphonomic research was conducted on carnivore bone modification (e.g. Sutcliffe 1970; Binford 1981; Brain 1981; Bunn 1982, 1983; Haynes 1983; Blumenschine 1986, 1988). This was largely due to the controversy generated by the interpretation of early archeological sites in East-Africa and South Africa, such as Olduvai Gorge (Tanzania), Koobi Fora (Kenya), Sterkfontein, Klasies River Mouth and Swartkrans (South Africa), among others. Opposing hypotheses were posited to explain the origin of bone assemblages in which hominins and carnivores were the major actors (e.g. Leakey 1971; Binford 1981, 1984; Brain 1981; Bunn 1982; Blumenschine 1986; Potts 1988; Turner 1989; Bartram and Marean 1999; Klein et al. 1999; Outram 2000). To address this issue several classic taphonomic features were explored to try to differentiate hominin and carnivore bone modification, e.g. presence of cut marks, frequency of tooth marks and percussion marks, age class selection, breakage patterns and skeletal part representation (e.g. Binford 1981; Brain 1981; Bunn 1982; Klein 1982; Shipman and Rose 1983; Blumenschine 1986, 1988, 1995; Bunn et al. 1986; Domínguez Rodrigo 1997). Shortcomings of the taphonomic variables (such as equifinality) along with biases in the archeological record have led to ongoing debate.

In this context, further neotaphonomic research has been developed to improve our knowledge of carnivores as taphonomic agents. For instance, the variability of hyenas as taphonomic agents was pointed out (Lam 1992) and some of the diagnostic criteria previously established to characterise hyenid accumulations were questioned (Pickering 2002). During the last 10 years, research has focused either on taphonomically understanding the less known hyenid species, e.g. the striped hyena (e.g. Andrews 2008; Fosse et al. 2010; Kuhn et al. 2010; Arriaza et al. 2018) and the brown hyena (e.g. Fosse et al. 2010; Kuhn et al. 2010; Fourvel et al. 2015), or on applying new taphonomic perspectives to revise some classic spotted hyena dens (Egeland et al. 2008).

Felids have also been a focal point of neotaphonomic research. One of the first researchers to focus on leopards was Brain (1981). His interest emerged from the study of tooth mark-bearing Australopith remains from the Cradle of Humankind in South Africa. Baboons are a regularly prey of leopards and can be used as a suitable analogy for the study of Australopith bone modification carried out by carnivores (Brain 1981). Building on seminal study, additional research concerning carnivore modification on baboons by leopards and hyenas has been conducted (e.g. Pickering 2001a, 2001b; Pickering et al. 2011). But neither Brain (1981) or Pickering et al. (2004) could undeniably show that leopards were the main accumulating agent of the Australopith remains from Sterkfontein, although a large carnivore was proposed as the more plausible agent.

Felids have also been relevant in the study of subsistence patterns of early hominins. As mentioned earlier, the co-occurrence of tooth marks, cut marks and percussion marks on bone remains from the FLK Zinj (Olduvai Gorge) has led to ongoing debate about whether or not early hominins were scavengers or hunters (e.g. Binford 1981; Bunn 1982; Blumenschine 1986, 1988; Bunn et al. 1986; Potts 1988). To test these relationships, several neotaphonomic models were developed to explore whether hominins scavenged carcasses from carnivore kills or obtained their prey by confrontational scavenging, or, in contrast, were primary hunters (e.g. Binford 1981; Bunn 1982; Blumenschine 1986, 1988; Bunn et al. 1986; Potts 1988). For instance, the availability of carcasses stored in trees from leopard kills was explored as a potential source of meat and marrow for scavenging hominins (Cavallo and Blumenschine 1989; Blumenschine and Cavallo 1992). Tooth and percussion mark frequencies on long bone specimens from the FLK Zinj led to hypothesize that hominins scavenged from felid kills and consumed abandoned flesh, marrow and brain. Thus, durophagous carnivores (e.g. hyenas, which are capable of breaking, open and consuming bones) may have been the last contributor in the modification sequence in depleting grease from long bone epiphyses (Blumenschine et al. 1994; Blumenschine 1995). This hypothesis was constructed without taking into account the cut mark frequency (Domínguez Rodrigo 1997, 2002; Domínguez-Rodrigo et al. 2007a). Along with this, some of the variables used, such as the frequency of tooth marks, showed the problem of equifinality: a low tooth mark frequency can be inflicted by a secondary access of hyenids or a primary access by felids (e.g. Domínguez-Rodrigo et al. 2007b). Further neotaphonomic experiments have been conducted to test the validity of Blumenschine's hypothesis involving scavenging hominin behaviour after lion (*Panthera leo*)

consumption of prey were conducted in the wild (Domínguez-Rodrigo 1999; Gidna et al. 2014). In addition to these studies, experiments with lions in a Game Reserve (Pobiner 2015) and with captive lions and tigers (*Panthera tigris*) were also conducted (Parkinson et al. 2015; Parkinson 2018). But results from these neotaphonomic studies and the interpretation of the early archeological record based on experimental outcomes remains controversial. This is partly due to shortcomings in the neotaphonomic frameworks established: sample size, the use of not-analogous prey and captive carnivores, the partial exploration of the carnivore guild, or the problem of the multi-agent scenario (several carnivore species involved) and the equifinality of some taphonomic variables (e.g. Gidna et al. 2013; Domínguez-Rodrigo et al. 2014).

Along with the taphonomic controversy found in African archaeological sites, several bone assemblages from the Iberian Peninsula have been interpreted as being accumulated by leopards, such as Los Rincones, S'Espasa Cave, Raco del Duc or Amalda (e.g. Yravedra 2010; Sauqué et al. 2014, 2018; Sauqué and Sanchis 2017). The accurate characterization of leopards as taphonomic agents is important because this species could have played an important role in the formation of archeo-paleontological sites. The distinction between felid bone modification and other carnivore groups, such as hyenids, is important in order to clearly address the taphonomic debate discussed above. Especially, because most of the early archeological sites are considered palimpsests in which several carnivore species could have been involved in bone accumulation and modification (e.g. Brain 1981; Domínguez-Rodrigo et al. 2007a).

Recently, methods have been developed to address some of the above problems. For example, integration of micro-photogrammetric techniques along with geometric morphometrics in the study of taphonomic marks has been shown to be effective in characterising cut marks (Mate-Gonzalez et al. 2015). Tooth marks (pits and scores) inflicted by different carnivore species such as the spotted hyena and lion have also been successfully distinguished through the use of these techniques (Aramendi et al. 2017; Arriaza et al. 2017; Yravedra et al. 2017; Horn 2018). The aim of this paper is to re-assess Bob Brain's neotaphonomic leopard collection through the application of these new techniques in order to morphologically characterise leopard tooth marks and combine these results with variables previously studied such as the frequency of tooth marks to try to avoid the problem of equifinality. The study of pit to score ratio has been also carried out. The potential application of these new techniques in early African archeological sites has been also explored.

## Material and methods

As mentioned in the introduction section, Bob Brain was a pioneer of the study of carnivore neotaphonomy. His interest in tooth mark-bearing Australopiths from the Cradle of Humankind in South Africa (Kromdraai, Sterkfontein and Swartkrans) led him to study several dens and to conduct experiments with leopards (Brain 1981). The material studied here was collected by Brain from four leopard dens and four carcasses from leopard kills (three impalas (*Aepyceros melampus*) and 1 steenbok (*Raphicerus campestris*)) from the Kruger

National Park (South Africa). These collections are housed at the Ditsong National Museum of Natural History in Pretoria (South Africa). For further details concerning the material see Brain (1981).

### Score to pit ratio

Following the criteria summarized by Blumenshine et al. (1996), all conspicuous and inconspicuous tooth marks on long bones were identified with the aid of a 20 x hand lens. The sample was classified according to tooth mark type (pits and scores) and bone density: cancellous bone (from epiphyseal sections) and dense cortical bone (from diaphyseal sections). Pits are described as tooth marks which contain bowl-shaped interiors and scores are characterised by U-shaped cross-sections (e.g. Binford 1981; Blumenshine 1995).

The score to pit ratio has been explored as a variable to discriminate bone modification inflicted by different carnivore species. While the frequency of scores is higher than the number of pits on long bone shafts in assemblages consumed by lions, hyenas and wolves generate balanced rates of pits and scores (Domínguez-Rodrigo et al. 2012).

### Microphotogrammetric reconstruction of tooth marks and geometric morphometric analyses

Forty one pits and 28 scores inflicted by leopards on baboons and size 1–2 ungulate long bones were analysed. First, morphological

**Table 1.** Tooth mark sample used in this study. Eleven ungulate long bones and three baboon long bones were used for the sample consumed by the leopard.

	Pits	Scores
<b>Leopard</b>	41	28
<i>on baboon</i>	13	11
<i>on bovid</i>	28	17
<b>Hyena</b>	21	33
<b>Lion</b>	24	30

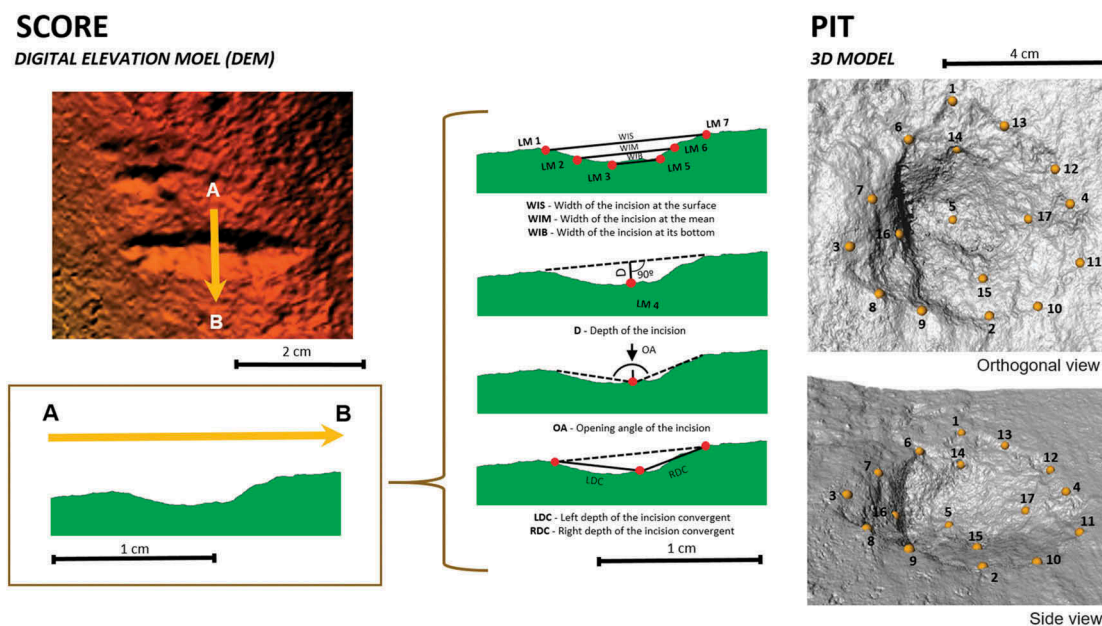
differences among the leopard pit and score sample were assessed to discuss possible discrepancies due to prey size and osteological properties of the different prey. Then, the leopard tooth mark sample was compared with tooth marks generated by hyenas and lions (Table 1) in a controlled setting at the Cabárceno Nature Park (Cantabria, Spain). Though carnivore behaviour might vary in captivity (e.g. Gidna et al. 2013; Arilla et al. 2014), the use of the Cabárceno sample is suitable because tooth mark morphology and size is not affected by the environment. For more details about the lion sample see Gidna et al. (2013), and for the hyena sample see Domínguez-Rodrigo et al. (2015).

High-resolution images of tooth marks were obtained through the use of a Canon EOS 700D reflex camera with 60 mm macro lens, following the methodology of Maté-González et al. (2015). Images were processed to generate a 3D model (Figure 1) for each tooth mark with the software GRAPHOS (inteGRated PHOtogrammetric Suite) (González-Aguilera et al. 2016).

### Scores

The morphology of the scores was analysed using two-dimensional cross-sections that are representative of the mark (Maté-González et al. 2015; Yravedra et al. 2017). Morphologic information was captured in two ways: first, seven bidimensional measurements were taken to capture size information on the score profiles (Figure 1); second, seven homologous points (landmarks) that contain morphologic information in the form of Cartesian coordinates, (O'Higgins and Johnson 1988; Bookstein 1991; Hall 2003; Klingenberg 2008) were used to describe the shape properties of the score cross sections (Figure 1, see Yravedra et al. 2017 for further details).

Measurements and landmarks were obtained using the open access software tpsDIG 2 (v.2.1.7) and were studied separately. Measurements were analysed by means of traditional multivariate statistics, while landmarks were used to perform geometric morphometric analysis based on a Procrustes superimposition, that normalizes the form information, and enables the use of



**Figure 1.** Description of the measurements and landmarks taken on the score cross-section profiles and of the 17-landmark model use to characterise carnivore pits.

common multivariate statistics (Rohlf 1999; Slice 2001; Richtsmeier et al. 2002).

The statistical analysis was performed in the free software R ([www.rproject.org](http://www.rproject.org), Core-Team 2015). The principal component analysis (PCA) functions included in the FactoMineR library (Lê et al. 2008) and the ggplot2 library (Wickham 2009) were used to explore the distribution of the sample. Additionally, PCA three-dimensional graphs were generated using the pca3d function (Weiner 2017) for visualization purposes.

The presence of defined groups was statistically tested using a multiple variance analysis (MANOVA) after defining the nature of the data distribution. For that purpose, the MVN package (Korkmaz et al. 2014) in the CRAN repository was used. When the condition of variance homogeneity was not fulfilled, the RVAdMemoire library (Hervé 2018) was preferred, as it includes variance analyses that do not assume multivariate normality or homogeneity.

Linear discriminant analysis (LDA) was performed to assess group assignation using the jackknife cross-validation method based on the calculation of confusion matrices. A priori established groups were tested using the lda function in the MASS library (Venables and Ripley 2002).

Landmark configurations were also imported into R and analysed using the geomorph (Adams and Otárola-Castillo 2013) and shapes (Dryden and Mardia 2016) packages. Apart from the generalized procrustes analysis (GPA) and PCA functions included in those libraries, shape changes were visualized with the aid of transformation grids (Bookstein 1989). PC scores were later extracted to examine variance (MANOVA) and the power of discrimination (LDA) between the different groups. These tests were performed using the same functions and packages specified above. The number of PC scores used to conduct the tests was limited to gain power performance after observing the correlation of the landmarks with each PC score and confirming that no important information was omitted.

### Pits

The analysis of the pits was performed directly on virtual models using 17 three-dimensional points that map the interior and exterior of the pit (Figure 1). Following the guidelines

established in Aramendi et al. (2017), each pit was landmarked in Avizo (Visualisation Sciences Group, USA). This set of fixed landmarks allows assessing the morphological differences that characterize each carnivore pit in a replicable way (Aramendi et al. 2017; Yravedra et al. 2018).

The geometric morphometric analysis of the pits was performed in the same manner as in the study of the scores using the geomorph and shapes packages. Alongside the morphometric analyses in shape space, form space – containing shape and size information – was investigated after re-scaling the data using the natural logarithm of Centroid Size for the leopard sample. The PC scores obtained were used to conduct MANOVA and LDA tests to determine if, on a statistical level, carnivores could be distinguished based on the pits they generate, and to evaluate the accuracy of the classification, respectively. The number of PC scores used for those tests was determined according to their significance and explanatory power.

## Results

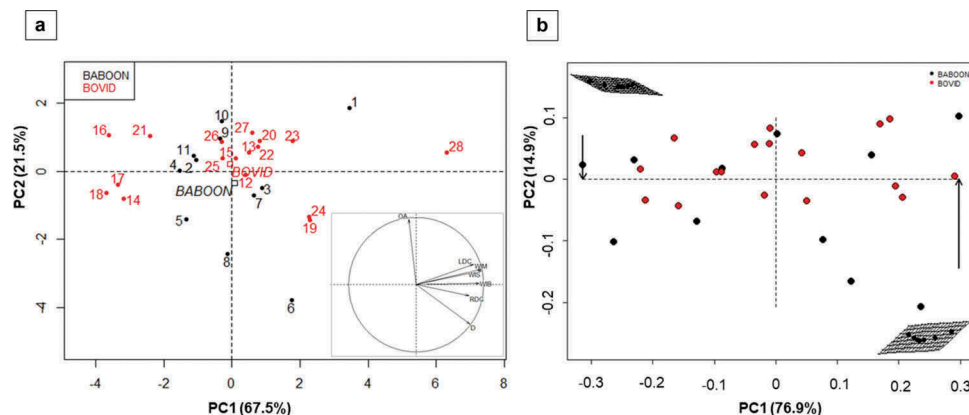
### Score to pit ratio

A total of 96 tooth marks (pits and scores) were localised on long bone shafts. Pits comprised 49% ( $n = 47$ ) and scores 51% ( $n = 49$ ). Scores show a higher incidence than pits, but the frequency is roughly balanced.

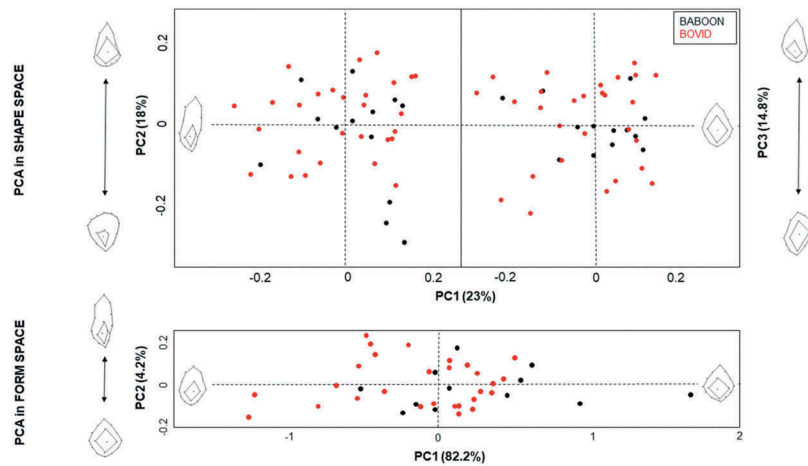
### Microphotogrammetric reconstruction of tooth marks and geometric morphometric analyses

#### Leopard tooth marks

The PCA plots generated for the leopard scores (Figure 2) and pits (Figure 3) reflect non-polarised morphospaces where the tooth marks observed on the carcasses of the baboons and ungulates cannot be separated at first glance. The morphometric information expressed in the plots ties in with the results obtained by means of MANOVAs: p values range between 0.12 and 0.55, confirming that there are no significant differences between the traces left by leopards on different species.



**Figure 2.** Scatter-plot of the PCAs for the linear and angular measurements and for the landmark data taken on the leopard score cross-section profiles. (a) The power of the different numeric variables is explained in the lower right corner. (b) Extreme shape changes described by PC1 are represented on the corresponding axis limit.



**Figure 3.** Scatter-plot of the PCA of the leopard pits in shape and form space. Extreme shape and form changes described by PC1 and PC2 are represented on the corresponding axis limit.

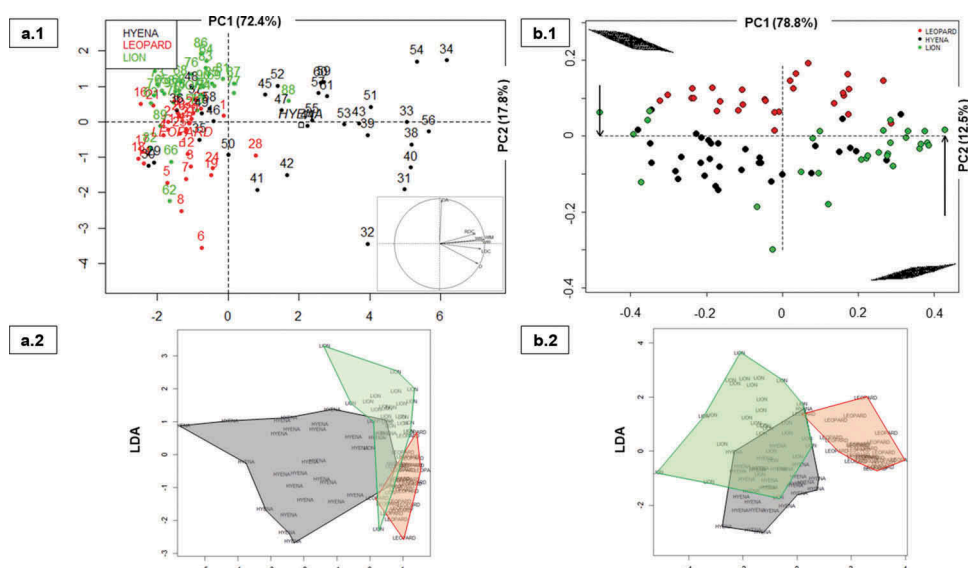
The LDA also shows high misclassification rates between the tooth marks on bovid and baboon carcasses (Table 3). Around half of the scores are incorrectly classified when considering the linear measurements and the shape characteristics. Pits seem to be more easily identifiable based on their morphology, since less than half of the total is misclassified. Whether these differences are related to more distinguishable morphologic patterns among pits or with larger differences in sample size (Table 1) needs to be further investigated. However, in the rest of the analysis we preferred to disregard the leopard pits on baboons, so as to avoid larger discrepancies and to limit the pit sample size to a number comparable to the rest of the carnivore pit samples.

#### Leopard vs hyena vs lion

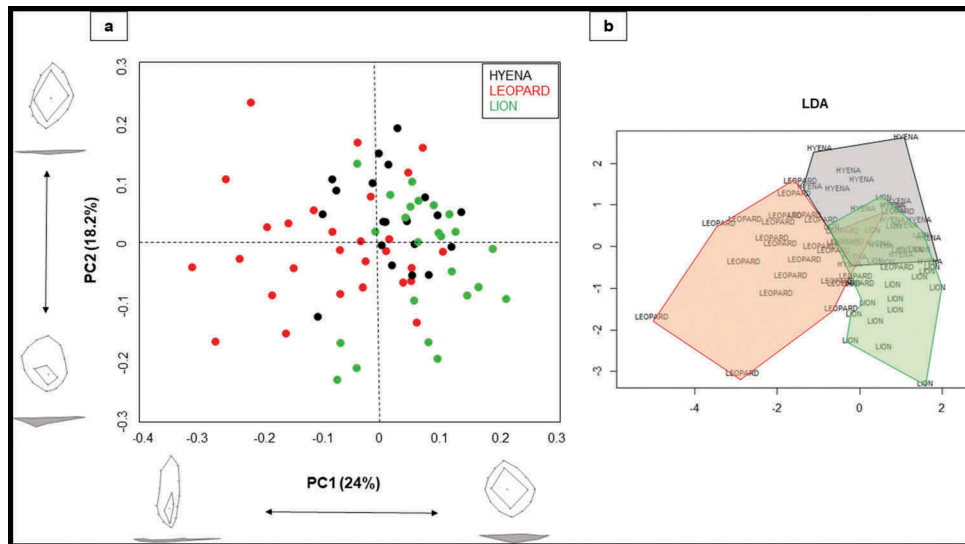
The PCA analyses of the tooth marks generated by leopards, hyenas and lions represented in Figures 4 and 5 show that these carnivores can be differentiated according to the traces they

leave on carcasses. The scatter-plot based on the measurements (Figure 4(a)) expresses more than 90% of the total sample variance. The first PC mainly explains the differences between scores inflicted by hyenas from the other two types. Leopard and lion scores overlap to a larger degree but there is a trend towards grouping along PC2, whereas hyenas seem to be uniformly distributed along this second PC. Changes in PC2 mainly correspond to differences in the opening angle of the scores, while the rest of the variables are contained in PC1. The scattering of the sample demonstrates that hyenas tend to generate a wider range of size patterns than lions and leopards.

When only shape attributes are considered, leopard scores can be better distinguished from hyenas and lions, which slightly overlap in the lower area of the graph (Figure 4(b)). However, scores generated by leopards and hyenas vary similarly along PC1 (with hyenas showing a slightly broader scattering), while those produced by lions tend to cluster at the extremes of the x axis.



**Figure 4.** Scatter-plot of the PCAs for (A.1) the linear and angular measurements and (B.1) for the landmark data taken on the leopard, hyena and lion samples. The LDA graphs depict the separation of the carnivore groups according to (A.2) the two-dimensional measurements and (B.2) shape features.



**Figure 5.** (a) Scatter-plot of the PCA of the leopard, hyena and lion pits in shape space with the extreme shape changes described by PC1 and PC2 represented on the corresponding axis limit. (b) The LDA graph depicts the separation of the carnivore groups according to shape features.

**Table 2.** Pairwise MANOVA results.

	Scores linear measurements		Scores landmarks		Pits	
	Hyenas	Lions	Hyenas	Lions	Hyenas	Lions
Leopards	0.001	0.001	0.001	0.001	0.002	0.001
Hyenas	-	0.001	-	0.001	-	0.02
Lions	-	-	-	-	-	-

These apparent differences are supported by the numeric results presented in Table 2 through  $p$  values that highlight significant differences between the carnivore groups.

The LDA scatter plots also stress the differences observed in the PCAs, showing a slight overlap between the scores when considering measurements and a clear separation of the leopard scores when using the landmark model. Classification tables (Supplementary file – Table SA) were calculated using the raw data for the classic method and the first 10 PC scores for the geometric morphometric approach, as they account for more than 90% of the total variance. The cross-validated LDA method is able to correctly classify around 80% of the scores in both cases (Table 3), leopards always being the easiest group to identify. The misclassification rates calculated for hyenas and lions are also quite low using both methodologies.

The analysis of the carnivore pits produced a poorly explanatory two-component plot where leopards appear separated from lions and hyenas (Figure 5). Therefore, a three-dimensional graph was produced to better visualize the distribution of the sample in a context where more than half of the total

variance is expressed (Supplementary File – GIF 1). The main differences between leopard pits and the rest of the sample are basically explained by changes along PC1. Lions and hyenas clearly overlap according to the morphology of their pits, but lions also generate pits with a smaller interior area in contrast to hyenas that generate more regular pits. The MANOVA results (Table 2) are capable of differentiating between carnivore groups, but the LDA performs slightly worse, with around 60% of the total pits correctly classified (Table 3). The percentages calculated for the probability of association are usually much higher in the case of lions and leopards (Supplementary File – Table SB). This might indicate that hyena pits present more difficulties when it comes to their morphometric definition, which is reflected in higher overlapping degrees in the LDA graph (Figure 5).

## Discussion

One of the early features used to differentiate felids and hyenids as taphonomic agents was the magnitude of bone modification (Brain 1981). Felids modify bone remains less intensively than hyenas (Brain 1981; Selvaggio 1994). For instance, long bone shafts consumed by lions rarely show more than 10 tooth marks (Gidna et al. 2014). The frequency of tooth marks inflicted by the leopard was examined in part of the collection re-studied in this paper, along with a baboon consumed by a cheetah and one lion kill (Dominguez-Rodrigo et al. 2007b). The number of tooth marks on complete long bones consumed by the leopard

**Table 3.** Results obtained from the LDA classification matrix after performing a jackknife cross-validation. The number of correctly identified marks is detailed next to the total number of marks for each sample.

	Pit shape	Pit form	Score based on measurements	Score shape
Test 1: <i>Leopard TM on baboon vs bovid</i>	Baboon: 2/13 Bovoid: 21/28 Total: 56.1%	Baboon: 2/13 Bovoid: 24/28 Total: 64.4%	Baboon: 4/11 Bovoid: 9/17 Total: 46.4%	Baboon: 6/11 Bovoid: 10/17 Total: 57.1%
Test 2: <i>Leopard TM vs Hyena TM vs Lion TM</i>	Leopard: 18/28 Hyena: 11/21 Lion: 15/24 Total: 60.3%		Leopard: 26/28 Hyena: 21/33 Lion: 25/30 Total: 79.1%	Leopard: 27/28 Hyena: 29/33 Lion: 21/30 Total: 84.6%

is usually less than 10, similar to lions and in contrast to hyenas (Domínguez-Rodrigo et al. 2007b) – although the frequency of tooth marks is higher when the long bone ends are consumed by the leopard (Domínguez-Rodrigo et al. 2007b). The low frequency of tooth marks on long bone shafts may be used to discern if a felid was the primary agent in the consumption process, but as mentioned previously, early archeological sites are palimpsests and more than one modifying agent should be expected. For this reason, this study also explored the frequency of tooth-marked specimens from these felid-derived carcasses after breaking bones with hammerstones, in order to replicate secondary access conducted by hominins (Domínguez-Rodrigo et al. 2007b). This was done to discern the frequency of tooth marks that should be expected in a scenario in which the leopard was the primary agent with hominins secondarily accessing the carcasses to get the marrow. This study assessed that long bone shafts in a felid-first experimental scenario showed a substantially lower percentage of tooth marks on small and medium-sized carcasses (<15%) as well as on large-sized carcasses (<22.2%) when compared to the carnivore (i.e. hyenid)-first model (80–100%) reproduced by Blumenshine (1988, 1995). Controversially, secondary access by hyenas to human-fractured bones results in low percentages of tooth-marked limb bone fragments (~20%) too and, more specifically, very low frequencies of tooth-marked midshaft fragments (10–15%) (Blumenshine 1988). Thus, it was concluded that the same low-frequency of tooth marks on shafts occurs in models where felids intervene first or in models where hyenids intervene secondarily to hominin-processed bone assemblages (Domínguez-Rodrigo et al. 2007b). The inability to recognise the carnivore taxa which produced the tooth marks, due to an overlap of tooth marks dimensions among large carnivore species (e.g. Domínguez-Rodrigo and Piqueras 2003; Delaney-Rivera et al. 2009; Andres et al. 2012), led to undermine the frequency of tooth marks as an accurate taphonomic variable to discern carnivore modification in a multi-agent scenario in which felids and hyenids could have intervened. Thus, only the frequency and location of human-derived marks such as cut and percussion marks could inform about the order access of hominins in the carcass consumption sequence (Domínguez-Rodrigo et al. 2007b). Results presented here show that, although some overlap is present, the three African carnivore species can be distinguished through the reconstruction of the morphology of tooth marks. In some of the analyses, leopard is the most discernible group. This poses a scenario in which tooth marks morphology can be used to discern the carnivore taxa involved in bone modification and the access order. By using this technique, a low tooth mark frequency now can be elucidated to have been made by a felid species or a hyena, so further interpretation about the access order of carnivores and hominins could be made in bone assemblages modified by both agents. Along with this, by applying this technique to any bone assemblage modified by carnivores the taxa involved could be elucidated. Thus, the application of this technique at archeo-paleontological sites such as Sterkfontein may discern what carnivore taxa were involved in bone modification and previous hypothesis can be tested.

To finally construct a neotaphonomic framework in which the analyses of tooth marks would help discern the carnivore

taxa involved in bone modification in a multi-agent scenario the score to pit ratio may be taken into account, not only the frequency and the morphology of tooth marks. The Syokimau spotted hyena den (Kenya) showed a 1:1 ratio (pit:score) (Egeland et al. 2008). This means that the spotted hyena inflicts a balanced number of both kinds of tooth marks during the consumption of its prey. This was further supported by comparisons made with bone assemblages consumed by the spotted hyena, lion and wolf (*Canis lupus*) (Domínguez-Rodrigo et al. 2012). The frequency of pits on long bone shafts consumed by the spotted hyena (56%) and wolf (51%) were higher than the frequency of scores, but roughly balanced. In contrast, the frequency of scores (>70%) in lion-derived assemblages was higher than the frequency of pits (Domínguez-Rodrigo et al. 2012). This fact was explained by the capability of hyenids and canids to inflict pressure on bones to break them, in contrast with strictly flesh-eating carnivores as lions (Campmas and Beauval 2008; Domínguez-Rodrigo et al. 2012). It could be expected that all felid species might inflict more scores compared to pits as the lion. This variable was also explored in baboon carcasses consumed by the leopard at the Mapungubwe National Park (South Africa) (Pickering et al. 2011). The average number of pit/scores per specimen (NISP) in baboon carcasses consumed by the leopard was > 2.5 (Pickering et al. 2011). However, some pits were interpreted as a possible secondary access by jackals because the length and breadth expanded the range of the dimensions of leopard tooth marks (Pickering et al. 2011). Interestingly, results presented here show that the ratio pit to score is balanced on long bones consumed by the leopard, similar to the frequency shown after wolf or spotted hyena consumption, and different to the frequency shown by the lion. As previously stated, the frequency of tooth marks inflicted by the leopard is higher when they consume the ends of long bones (Domínguez-Rodrigo et al. 2007b). This fact may also explain why the leopard shows a balanced pit to score ratio in contrast with lions, which focus on specific parts of the epiphyses (Domínguez-Rodrigo et al. 2015) rather than consume the complete end of the long bones like leopards, which, in doing so, inflict more tooth marks to completely break the shaft circumference. Additionally, the ratio score to pit published by Pickering et al. (2011) could have been generated by the leopard, but the tooth mark dimension still raises issues concerning the agency of tooth marks smaller than the dimensions usually inflicted by the leopard.

Thus, the combination of the tooth mark frequency, score to pit ratio and morphological reconstructions bring back the analyses of tooth marks as part of the identification of carnivore taxa involved in bone modification, not only in assemblages primarily accumulated by carnivores, but also in palimpsests in which several agents intervened (other carnivore species or hominins).

## Conclusions

During the last decades several taphonomic variables have been explored to characterise carnivore-inflicted bone modification. Some of them showed the problem of equifinality such as the frequency of tooth marks on shafts, or pit and



score dimensions. The application of new techniques, such as microphotogrammetry and geometric morphometrics, allow characterization of morphological variability among different taxa such as the spotted hyena, lion and leopard, overcoming the equifinality problem. The opportunity to distinguish tooth marks carried out by, at least, three African carnivore species, opens up the opportunity to deeply understand the formation process of archeo-paleontological sites in which carnivores were involved, such as Olduvai Gorge or Sterkfontein (work in progress). Other taphonomic variable previously described in lions and spotted hyenas such as the ratio pit to score has also been explored. The ratio score to pit inflicted by the leopard is balanced, similar to hyenas and wolves and contrary to lions. This leads us to think that not all taphonomic signals are shared by all felid species. Differences in bone density do not generate statistical differences between leopard tooth mark morphology on bovid vs baboon carcasses contrary to skeletal part representation deletion when leopards consume these two different kinds of prey. Thus, bone density or other prey constrains may skew some taphonomic variables but may not affect others. Therefore, neotaphonomic research must be constructed taken into account these concerns to accurately face the interpretation of the archeo-paleontological site formation processes.

Photogrammetry has been revealed as a promising technique for reconstructing taphonomic marks that can help solve certain taphonomic problems, as the one discussed here. Nevertheless the use of this methodology entails some disadvantages, such as long data collection and processing time. New methodological approaches based on the use of a structured light scanner (SLS) are trying to address these constraints (Maté-González et al. 2017). Along with this, the use of machine learning methods is refining the classification rates between groups (Courtenay et al. 2019).

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