Archaeol Anthropol Sci (2012) 4:209–219
DOI 10.1007/s12520-012-0093-4

ORIGINAL PAPER

A study of dimensional differences of tooth marks (pits and scores) on bones modified by small and large carnivores

Miriam Andrés · Agness O. Gidna · José Yravedra · Manuel Domínguez-Rodrigo

Received: 12 December 2011 / Accepted: 2 March 2012 / Published online: 20 April 2012

Abstract The use of tooth mark sizes to infer carnivore types when analyzing the modification of faunal assemblages has been criticized on the base of intense overlap in tooth mark size among differently sized carnivores. The present study analyzes this overlap and presents some critical explanations for it. This work is based on the largest collection of tooth pit dimensional data collected to date for some of the most relevant carnivore types. The study empirically shows that small and large carnivores can be clearly differentiated when using tooth pit size, with a higher discrimination when using tooth marks on dense shafts than on cancellous ends. It is argued that most previous studies of tooth mark sizes have reproduced a higher overlap probably because sample sizes were small, and experiments were carried out using small carcasses (which require a smaller bite force) or for a combination of factors.

Keywords Tooth mark · Tooth pit · Tooth score · Taphonomy · Carnivore

Introduction

Actualistic studies on hyenas (Brain 1981; Blumenschine 1986; Domínguez-Rodrigo 1993; Faith 2007), leopards (Sutcliffe 1973; Brain 1981; Cavallo 1998; Cavallo and Blumenschine 1989; Ruiter and Berger 2000; Pickering et al. 2004; Domínguez-Rodrigo et al. 2007a, b), lions (Domíguez-Rodrigo 1999a), pumas (Nasti 1996; Borrero et al. 2005; Montalvo et al. 2008; Muñoz et al. 2008), lynxes (Lloveras et al. 2008), foxes (Estévez and Mamelli 2000; Mondini 2000), wolves (Haynes 1980a, b, 1982; Yravedra et al. 2011), and bears (Pinto-Llona et al. 2005) have contributed to our understanding on carcass consumption and bone modification patterns by these potential taphonomic agents.

Given the diversity of body sizes and dentition sizes of all these mammalian carnivores, it has been argued that tooth mark sizes could potentially be used to differentiate carnivore types (Selvaggio and Wilder 2001; Dominguez-Rodrigo and Piqueras 2003; Delaney-Rivera et al. 2009). Selvaggio and Wilder (2001) showed some optimism when they used mark shape (ratio of major axis to minor axis of mark) and size (area in millimeters) to differentiate functionally different carnivore types (e.g., felids from hyenids), by using tooth pit properties on cancellous (epiphyseal), thinning cortical (metadiaphyseal), and dense cortical (diaphyseal) bone. This optimism recently received a further boost from experimental work showing that human-inflicted tooth marks could be differentiated from those of other carnivores (Fernández-Jalvo and Andrews 2011). A study of carnivore punctures carried out by Andrews and Fernández-Jalvo (1997) was used to infer more than one type of carnivore modifying the Sima de los Huesos hominin remains. Andrews and Fernández-Jalvo (1997) also showed that tooth pits could vary in size depending on element type. Despite this potential confounding factor, Andrews and Fernández-Jalvo (1997) divided carnivore damage according to mark size into three types: small (<1 mm), mixed (small or large carnivore) (1–4 mm), and larger carnivores (>4 mm). This latter assertion

M. Andrés · J. Yravedra · M. Domínguez-Rodrigo (✉)
Department of Prehistory, Complutense University,
Prof. Aranguren s/n,
28040 Madrid, Spain
e-mail: manueldr@ghis.ucm.es

A. O. Gidna · M. Domínguez-Rodrigo
IDEA (Instituto de Evolución en África),
Museo de los Orígenes, Plaza de San Andrés 2,
28005 Madrid, Spain

was further supported by Dominguez-Rodrigo and Piqueras (2003) who argued that tooth pit sizes could be used to differentiate small from large carnivores, but tooth marks were ambiguous to differentiate specific carnivore taxa. Andrews and Fernández-Jalvo (1997) were attributing carnivore sizes to tooth mark sizes expressed in their most frequent absolute values (mode) and their ranges, whereas Dominguez-Rodrigo and Piqueras (2003) were attributing carnivore size according to sample deviation from the mean values, assuming that the same teeth would generate homogeneous and a rather limited range of tooth mark sizes according to tooth size and the strength applied in bone gnawing. For this purpose, these authors were using mean values and 1 standard deviation (as initially suggested by Selvaggio 1994). While Andrews and Fernández-Jalvo's (1997) approach could be used for isolated marks on bones, Domínguez-Rodrigo and Piqueras' (2003) approach required its application to full samples, not isolated marks.

Recently, dimensional data collected from feeding experiments with a wider array of carnivores showed a much greater overlap in tooth pit dimensions irrespective of carnivore size and taxon (Delaney-Rivera et al. 2009). Marks on shaft sections of long bones showed the highest degree of ambiguity, whereas marks on cancellous portions showed a positive correlation with carnivore body mass. Although the experimental work of Delaney-Rivera et al. broadly agreed with Domínguez-Rodrigo and Piqueras' (2003) scheme of three carnivore groups, the greater overlap documented by Delaney-Rivera et al. made these authors argue for caution when interpreting carnivore type based on tooth pit sizes alone. Despite this caution, Delaney-Rivera et al. (2009) used diaphyseal tooth pits to differentiate three carnivore types: Pits <2 mm were attributed to small carnivores and medium-sized felids (Domínguez-Rodrigo and Piqueras' (2003) and Andrews and Fernández-Jalvo's (1997) threshold for this group was 4 mm), although several pits made by lions and tiger would also fall within this size range; pits between 2 and 4 mm were documented in a variety of medium and larger carnivores, and pits >4 mm were observed in larger carnivores (e.g., hyenas, lions, and large dogs).

In sum, all these studies seemed to succeed in showing a correlation of carnivore size and tooth pit sizes after certain thresholds. Small carnivores only make small tooth marks. Larger carnivores are capable of inflicting small as well as larger marks. Whereas attributing single marks to specific carnivore groups remains problematic because this will be done more confidently with larger marks (by excluding smaller carnivores), most marks <4 mm cannot be reliably attributed to any specific carnivore group.

The present study was conducted with the goal of expanding these inferences with a larger sample of tooth marks. Sample sizes for tooth pits per bone section compiled by Delaney-Rivera et al. (2009) were very small (in most cases <20 marks per bone section per carnivore type), as were those compiled for certain carnivores by Domínguez-Rodrigo and Piqueras (2003) (e.g., <15 marks per bone section for lions). Small samples prevent the understanding of the authentic ranges of variation in the size of marks potentially created by each carnivore type. The present analysis will include the largest sample of tooth marks per bone section for the some of the most important carnivores potentially interacting with hominins in the formation of the Pleistocene archeological record.

Sample and method

Although tooth marks have been documented as occurring in diverse forms (pits, scores, punctures, and furrowing) (Binford 1981), the present study will focus on two types (pits and scores), which are the tooth mark types previously studied by other researchers (Selvaggio and Wilder 2001; Dominguez-Rodrigo and Piqueras 2003; Delaney-Rivera et al. 2009). These tooth marks are described by Blumenschine (1995: 29) as having "bowlshaped interiors (pits) or U-shaped cross-sections (scores) that commonly show crushing that is conspicuous under the hand lens, and which, macroscopically, gives the mark a different patina than the adjacent bone surface." (Fig. 1).

Part of the faunal collection used by Domínguez-Rodrigo and Piqueras (2003) was re-analyzed in the present study. It comprised bones modified by baboons, dog (German shepherd), spotted hyenas, and lions. To this, we have added new faunal assemblages from carcasses consumed by foxes, wolves, humans, spotted hyenas, as well as a substantially enlarged sample of bones from carcasses consumed by lions (including more than 400 tooth marks). The reason for re-analyzing Domínguez-Rodrigo and Piqueras' (2003) collection was strictly methodological. In their previous study, Domínguez-Rodrigo and Piqueras (2003) only measured conspicuous marks. Several inconspicuous marks were not included in the analysis. Inconspicuous marks are different from conspicuous marks because they require some magnification to be properly identified (Blumenschine 1988, 1995); they therefore are mostly small marks. In the present study, *all* marks were microscopically identified and measured, which implies that a substantial amount of small marks were added to the previous analyzed sample.

Marks were obtained from bones fed upon (in fleshed state) by lions and spotted hyenas and (in defleshed state, bearing only minor flesh scraps) by dogs and baboons. The sample of tooth-marked bones from lions in Domínguez-Rodrigo and Piqueras' study was obtained in the northern Maasai Mara National Reserve (Kenya) (Domíguez-

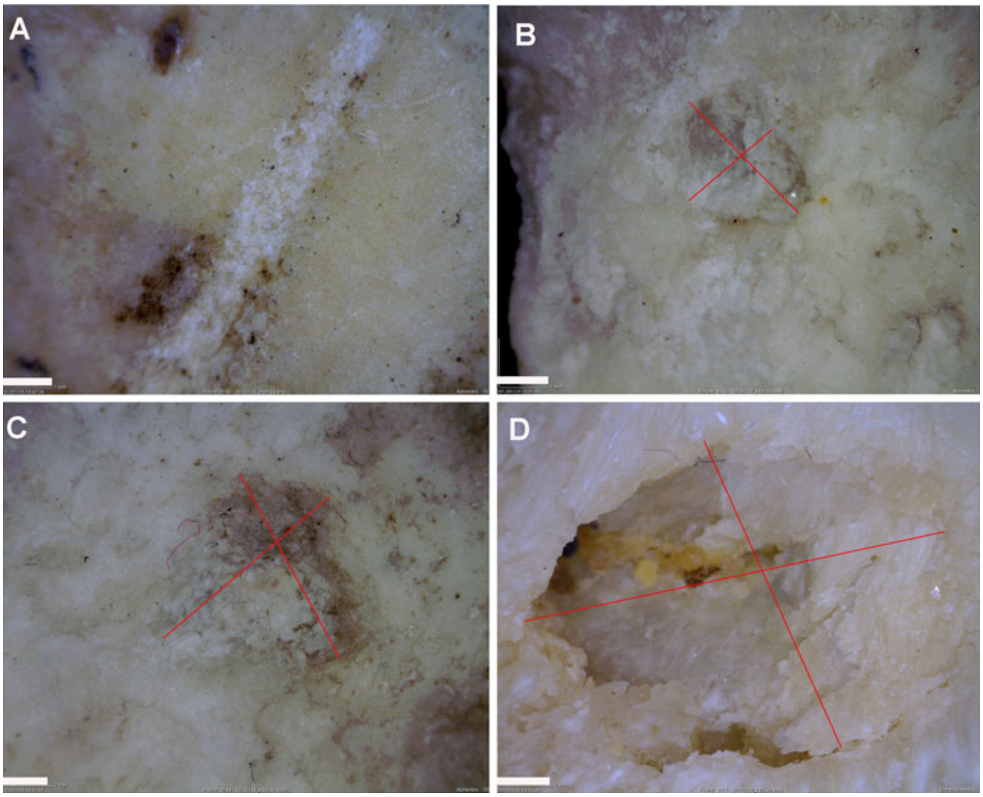

Fig. 1 **a** Tooth score on dense bone; **b** tooth pit on dense bone showing the typical oval shape; **c** tooth pit on dense bone showing an irregular outline; **d** tooth pit on cancellous bone. This shows part of the variability of tooth pit shapes and the way they were measured (in *red*): length (major axis), breadth (minor axis). Tooth pit in D shows the outline defined by the crushing of the bone with the outer cortical layer flaked and exposed and the inner pit defined by the depression into cancellous bone. *Scale bar*= 1 mm

Rodrigo 1999a). The present analysis includes tooth marks from carcasses consumed by lions in Tarangire (Tanzania) (work in progress). Tooth-marked bones from hyenas were obtained in one experiment documenting carnivore ravaging of a human-made assemblage in Galana and Kulalu (Domínguez-Rodrigo and Martí 1996). Bones modified by baboons were obtained from a study conducted in the Barcelona zoo (Spain) (Domínguez-Rodrigo et al. 1998) and at Tsavo East (Domíguez-Rodrigo 1999b). Bones gnawed by dogs were obtained in feeding experiments with German shepherds (*Canis familiaris*) (Dominguez-Rodrigo and Piqueras 2003). The new carnivore samples included in the present study were obtained from wild wolves in northern Spain (Yravedra et al. 2011), humans (collection of bones chewed by Maasai morani at Maritanane, Peninj, Tanzania), wild foxes from Ayllón (Segovia, Spain) (work in progress), a spotted hyena den (Kisima Ngeda Den 2) found in Eyasi (Tanzania) (Prendergast and Domínguez-Rodrigo 2008), and some marks on a selected sample of bones from the Maasai Mara spotted hyena den (Kerbis-Peterhans 1990). Since marks on the Eyasi hyena den sample were probably made by pups, we decided to split the hyena sample in two: that from the hyena den and those from the samples made by adult hyenas. Although humans and baboons are not strict carnivores but rather omnivores, we classify them as carnivores in the present study for the sake of comparative purposes, given their ability to modify bones while consuming carcass remains. Carnivores were divided into two size categories: small and large (see Delaney-Rivera et al.'s (2009) Table 1). Here we consider any carnivore under 40 kg to be small. Humans, given their overall small-sized dentition when compared to other carnivores, were also classified as small despite their larger body size.

Most carcasses used for these experiments are medium-sized, belonging to either bovids or equids. Only the bulk of bones fed upon by spotted hyenas at the Eyasi den were from small-sized carcasses (Bunn's (1982) size 1). Bones tooth-marked by foxes were also small (six sheep carcasses). Only long bones were used in the present study. Marks were documented on dense cortical bone (shafts) and on cancellous bone (ends). The metadiaphyseal sections were not documented because their thickness varied according to element and these sections do not systematically sample bone thickness intermediate between end and mid-shafts. Marks were spotted with hand lenses (15–20×), and both conspicuous and inconspicuous marks were measured. Measurements were taken using lenses and an electronic caliper on marks instead of on molds. Length (maximum dimension) and breadth (maximum dimension transversal to length) of tooth pits and tooth scores were taken. Sample sizes for each carnivore species are shown in Tables 1 and 2.

Marks were measured including a perimeter marked by any modification of the original cortical surface. This includes mark edge flaking, since the control of the sample allowed one to ascribe this modification to carnivores and not to any non-biotic agent.

Table 1 Dimensions (length and breadth) of tooth pits in the carnivore sample used. Data include mean values, 95% confidence interval, standard deviation and minimum and maximum values documented in each sample

	n	Mean	95 % confidence interval lower	95 % confidence interval upper	SD	Min	Max
Hyena[a] shaft breadth	46	1.55	1.2	1.9	1.2	0.21	8.7
Hyena[a] shaft length	46	2.71	1.81	3.41	3.11	0.33	9.1
Hyena[a] end breadth	17	2.9	1.6	4.2	2.73	0.11	14
Hyena[a] end length	17	5.4	2.9	7.9	5.1	0.3	25.6
Hyena[b] shaft breadth	456	1.19	1.12	1.26	0.75	0.15	6.52
Hyena[b] shaft length	456	1.57	1.48	1.66	0.98	0.17	11.3
Hyena[b] end breadth	260	1.64	1.49	1.79	1.24	0.23	11
Hyena[b] end length	260	2.39	2.59	2.19	1.64	0.31	20.8
Wolf shaft breadth	236	1.8	1.69	1.91	0.87	0.16	7.48
Wolf shaft length	236	2.49	2.34	2.64	1.15	0.4	9.41
Wolf end breadth	129	2.7	2.48	2.92	1.25	0.83	7.41
Wolf end length	129	3.61	3.33	3.9	1.63	1.04	9.95
Fox shaft breadth	67	0.99	0.77	1.2	0.87	0.19	5.91
Fox shaft length	67	1.54	1.25	1.83	1.18	0.36	6.52
Fox end breadth	41	1.88	1.54	2.22	1.08	0.8	5.26
Fox end length	41	2.56	2.08	3.03	1.5	0.99	9.07
Maasai shaft breadth	31	0.76	0.58	0.93	0.47	0.14	2.57
Maasai shaft length	31	1.06	0.85	1.27	0.57	0.39	2.96
Maasai end breadth	14	0.91	0.6	1.23	0.55	0.35	2.31
Maasai end length	14	1.25	0.83	1.66	0.71	0.42	2.79
Baboon shaft breadth	66	0.8	0.71	0.89	0.35	0.31	5.39
Baboon shaft length	66	0.94	0.82	1.06	0.48	0.31	6.08
Baboon end breadth	36	1.66	1.26	2.05	0.37	1.01	5.55
Baboon end length	36	1.76	1.26	2.25	0.47	1.01	9.9
Dog shaft breadth	66	1.36	1.2	1.52	0.66	0.5	4.28
Dog shaft length	66	1.77	1.54	1.99	0.91	0.5	6.32
Dog end breadth	19	1.9	1.53	2.27	0.76	0.75	7.93
Dog end length	19	2.4	1.85	2.95	1.14	1.03	9.88
Lion shaft breadth	28	1.7	1.49	1.91	1.41	0.6	7.25
Lion shaft length	28	2.87	2.2	3.54	1.8	1.29	9.2
Lion end breadth	178	4.05	3.7	4.39	2.37	0.74	15
Lion end length	178	6.17	5.08	7.25	3.51	0.98	23.3

[a] Maasai Mara hyena den

[b] Eyasi hyena den

Contrary to Domínguez-Rodrigo and Piqueras' (2003) statistical treatment of data, which included mean and deviation values, the present study has used a trimmed mean (5 %), which is enough to prevent the few extreme outliers from biasing the mean and standard deviation values. Thus, somewhat smaller values than those reported by Domínguez-Rodrigo and Piqueras were obtained, which has as much to do with removing the outliers as with including a large portion of previously non-reported inconspicuous marks. The novelty in the statistical treatment of data is that instead of 1 standard deviation (representing variation on 68 % of the sample on both sides of the mean), a 95 % confidence interval was used, representing the variation of most of each sample. To elaborate the confidence interval, a two-tailed alpha value of 0.025 was used.

Results

A Mann–Whitney–Wilcoxon test shows that there are significant differences when comparing the length ($p=0.032$) and breadth ($p=0.028$) of pits on ends and the length ($p=0.029$) and breadth ($p=0.006$) of pits on shafts in the lion samples reported by Dominguez-Rodrigo and Piqueras (2003) and in the present study. Likewise, statistical differences in these dimensions and portions ($p=<0.020$) have been documented for the spotted hyena and baboon samples reported by Dominguez-Rodrigo and Piqueras (2003) and those shown here for the same taxa. This indicates that the inclusion of inconspicuous marks has affected the mean values and the sample dispersion as they were reported in previous research.

Table 2 Dimensions (length and breadth) of tooth scores in the carnivore sample used. Data include mean values, 95% confidence interval, standard deviation and minimum and maximum values documented in each sample

	n	Mean	95 % confidence interval lower	95 % confidence interval upper	SD	Min	Max
Hyena[a] shaft breadth	603	0.6	0.55	0.65	0.63	0.1	8.1
Hyena[a] shaft length	603	3	2.83	3.16	2.01	0.35	31.6
Hyena[a] end breadth	542	0.66	0.6	0.72	0.73	0.11	9
Hyena[a] end length	542	3.6	3.35	3.85	3.01	0.39	25.2
Wolf shaft breadth	306	1.68	1.56	1.81	1.12	0.12	7.8
Wolf shaft length	306	8.62	8.13	9.1	4.31	1	32.03
Wolf end breadth	78	2.92	2.55	3.29	1.63	1	7.91
Wolf end length	78	10.76	9.64	11.88	4.97	3	23.37
Fox shaft breadth	96	0.42	0.36	0.49	0.32	0.11	2.02
Fox shaft length	96	3.64	3.21	4.07	2.1	1.36	14.22
Fox end breadth	7	0.65	0.28	1.02	0.4	0.32	1.23
Fox end length	7	3.71	2.62	4.79	1.17	2.48	6.03
Maasai shaft breadth	18	0.56	0.42	0.71	0.29	0.19	1.1
Maasai shaft length	18	1.91	1.46	2.36	0.9	0.77	4.65
Maasai end breadth	14	0.46	0.28	0.65	0.31	0.18	1.47
Maasai end length	14	2.34	1.24	3.45	1.91	0.96	7.42
Baboon shaft breadth	96	0.46	0.42	0.5	0.19	0.11	3.53
Baboon shaft length	96	2.77	2.37	3.17	1.98	0.63	17.85
Baboon end breadth	12	0.67	0.38	0.97	0.46	0.18	4
Baboon end length	12	3.98	2.7	5.26	2.01	1.56	5.5
Dog shaft breadth	164	0.66	0.61	0.71	0.3	0.14	3.49
Dog shaft length	164	5.06	4.63	5.49	2.76	1.14	26.55
Dog end breadth	45	0.81	0.7	0.92	0.36	0.14	4.58
Dog end length	45	5.95	5.08	6.82	2.9	2.19	21.48
Lion shaft breadth	124	0.96	0.86	1.06	0.58	0.26	3.66
Lion shaft length	124	9.32	7.45	11.19	5.05	2.7	26.45
Lion end breadth	76	2.7	2.32	3.08	2.59	0.5	18.8
Lion end length	76	10.68	9.55	11.8	5	3.07	35

Data include mean values, 95 % confidence interval, standard deviation, and minimum and maximum values documented in each sample

[a] Eyasi spotted hyena den

The analysis of pits reveals that some differences can be documented between small and large carnivores (Table 1). When documenting pit sizes on ends (Fig. 2), no clear distinction exists when using pit length. There is a strong overlap between small carnivores and omnivores, such as humans and foxes (see the uppermost value documented for jackals) and larger carnivores, such as dogs and wolves. This overlap is even stronger when comparing pit breadth on ends (Fig. 3), where the 95 % confidence interval of the dog sample is similar to those documented for foxes and even baboons. The maximum boundary of the confidence interval of jackal also embodies all carnivores, except the uppermost range of adult spotted hyenas. This supports Domínguez-Rodrigo and Piqueras' (2003) interpretation of ambiguity in the differentiation of carnivores when using cancellous shafts and shows a lower boundary (4 versus 5 mm) for pit length and for pit breadth (3.2 versus 4 mm) when comparing both sets of carnivores. Therefore, when tallying complete sets of tooth pits on ends, differentiation is rather ambiguous and only lions and hyenas seem to be clearly differentiated in marks that are on average larger than 4 mm. This boundary is the same that Delaney-Rivera et al. (2009; Fig. 5) documented as separating large mammal carnivores from smaller ones.

Small carnivores and omnivores (subadult hyenas, foxes, humans, and baboons) can be better differentiated from larger carnivores (adult hyenas and wolves) when comparing pit length on dense cortical shafts (Fig. 4). The only dubious carnivore is the dog, which overlaps in its lowest range with the smaller carnivores. However, a boundary of 1.8 mm seems to be a good discriminator between large and small carnivores. This overlap of dogs with smaller carnivores is dissipated when using pit breadth on shafts (Fig. 5), which shows that after a threshold of 1.25 mm, pits made by larger carnivores can be differentiated from smaller ones. The 1.8-mm pit length boundary to separate large mammalian carnivores from smaller ones was documented by Delaney-Rivera et al. (2009; Fig. 6) as more effective after 2 mm.

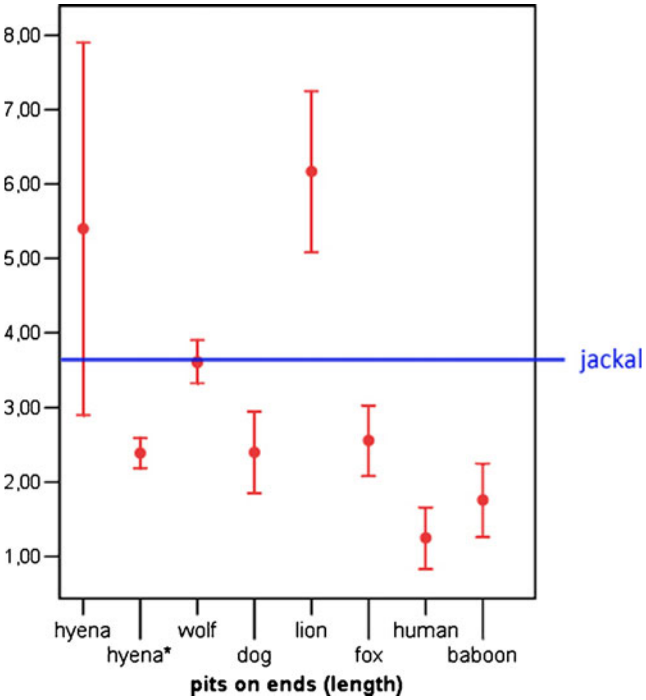

Fig. 2 Mean values and 95 % confidence intervals of tooth pit length (millimeters) on cancellous ends. They were calculated using the t distribution, where $t \cdot 0.025$ is the critical value of t with $n-1$ degrees of freedom. The maximum value documented for the range of jackals is shown in the form of *horizontal line*, which approximates the boundary separating small from larger carnivores. "Hyena" refers to the Maasai Mara den sample (*large carcasses*) and "Hyena*" refers to the Eyasi den sample (*small carcasses*) (see differences in text)

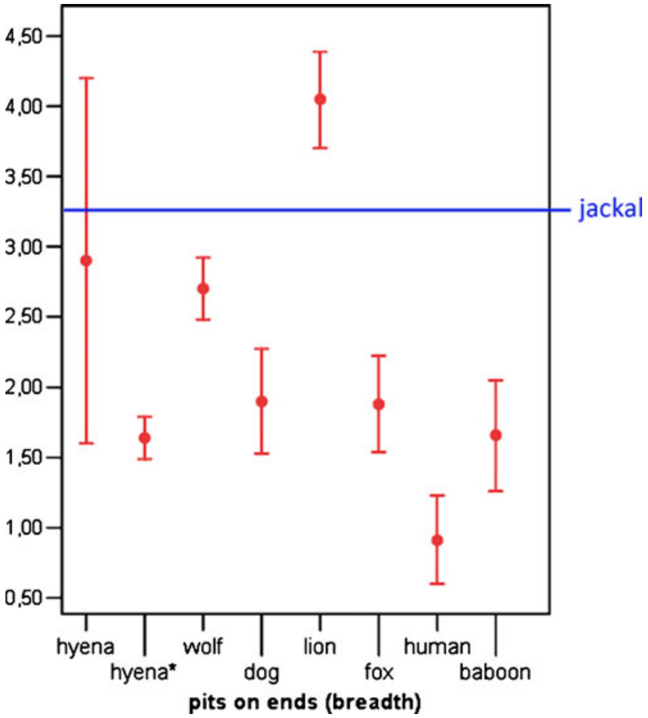

Fig. 3 Mean values and 95 % confidence intervals of tooth pit breadth (millimeters) on cancellous ends. They were calculated using the t distribution, where $t \cdot 0.025$ is the critical value of t with $n-1$ degrees of freedom. The maximum value documented for the range of jackals is shown in the form of *horizontal line*, which approximates the boundary separating small from larger carnivores. "Hyena" refers to the Maasai Mara den sample (*large carcasses*) and "Hyena*" refers to the Eyasi den sample (*small carcasses*) (see differences in text)

Domínguez-Rodrigo and Piqueras (2003) were skeptical that scores could be used in a meaningful way to differentiate among carnivore types because score length was highly variable within a single agent. However, while the score length is subjected to wide variability (depending on the bite type, portion of the bone, bone size, force of bite, and other variables), the score breadth could potentially reflect more faithfully the size of the tooth that inflicted the mark and, hence, the size of the carnivore. Table 2 shows data for scores per carnivore type. Figure 6 shows how score breadths on ends discriminate between small carnivores (subadult hyenas, foxes, humans, baboons) and large carnivores (lions and wolves) (no data were taken on the Maasai Mara spotted hyena sample). Dogs appear again as outliers. This applies also to score breadths on shafts (Fig. 7).

Discussion

Delaney-Rivera et al. (2009) argued that there was a strong overlap in tooth mark dimensions within a large set of carnivores. Despite this, they posited that small- and medium-sized and large carnivores could be differentiated when using pits on shafts. The overlap was accounted for larger carnivores inflicting small and larger marks when they exerted less or more force on bone. The present study shows that this purported overlap in tooth pit dimensions can have more reasons other than carnivore size alone. For instance, statistical overlap, either using standard deviation or confidence intervals, is highly dependent on sample size. Most statistical tests used for inter-sample comparison of numeric variables require samples larger than 30 components for reliable inferences (Hair et al. 1998; Lewis and Traill 1999; Wilcox 2005). Delaney-Rivera et al. (2009) used 60 tooth mark sets (one per agent) divided into bone portions (epiphysis, metadiaphysis, diaphysis) and tooth mark type (pits, scores), out of which only five of these subsets had more than 30 tooth marks represented. This subsample of >30 components makes up a small fraction (8.3 %) of the total sample used. Therefore, the strong overlap documented by Delaney-Rivera et al. (2009) may have something to do with sample sizes in addition to the effect of carnivore type in each of them. This is further supported by the fact that the range of tooth pit dimensions documented in the present study for the first hyena sample (Maasai Mara hyena den) is significantly wider than that reported for the second hyena sample (Eyasi hyena den),

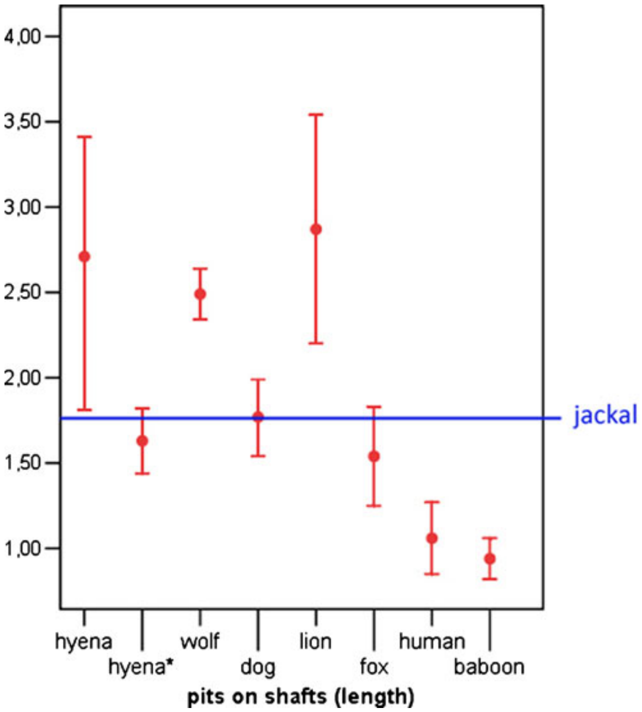

Fig. 4 Mean values and 95 % confidence intervals of tooth pit length on dense shafts. They were calculated using the *t* distribution, where *t*·0.025 is the critical value of *t* with *n*−1 degrees of freedom. The maximum value documented for the range of jackals is shown in the form of *horizontal line*, which approximates the boundary separating small from larger carnivores. "Hyena" refers to the Maasai Mara den sample (*large carcasses*) and "Hyena*" refers to the Eyasi den sample (*small carcasses*) (see differences in text)

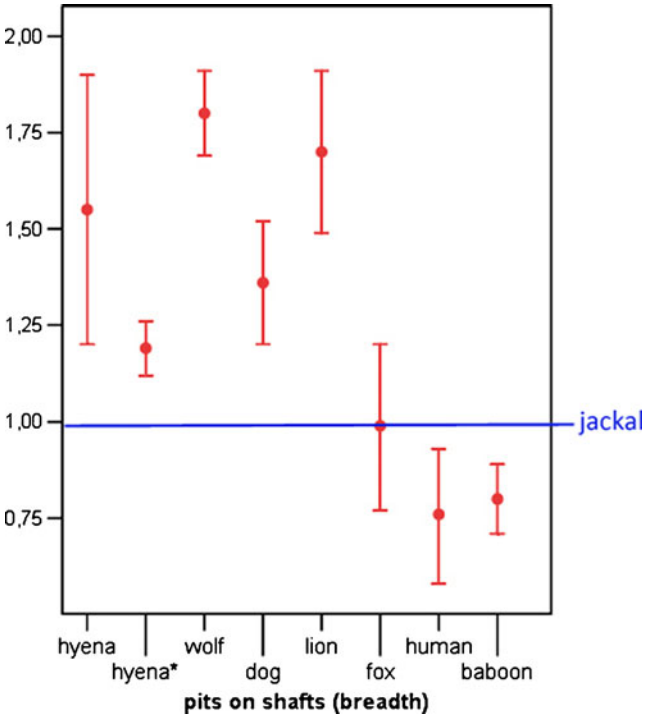

Fig. 5 Mean values and 95 % confidence intervals of tooth pit breadth (millimeters) on dense shafts. They were calculated using the *t* distribution, where *t*·0.025 is the critical value of *t* with *n*−1 degrees of freedom. The maximum value documented for the range of jackals is shown in the form of *horizontal line*, which is slightly lower than the boundary separating small from larger carnivores. "Hyena" refers to the Maasai Mara den sample (*large carcasses*) and "Hyena*" refers to the Eyasi den sample (*small carcasses*) (see differences in text)

probably because the sample size of the former is about one tenth of the sample size of the latter.

In addition, another variable introduced experimentally by Delaney-Rivera et al. (2009), which may have affected the outcome, is that *all* carnivores, of all sizes, were fed defleshed goat limbs (only on a third trial were some carnivores presented with a cow femur). Feeding on a small carcass requires little bite force from carnivores and especially from the larger ones. Consequently, the resulting tooth marks do not need to be big. What Delaney-Rivera et al. (2009) could have successfully documented with such an experimental variable is that small and large carnivores might show a stronger overlap of the size of tooth marks they inflict on bone surfaces when they feed on small carcasses. However, given that each carnivore type has a different predatory range expressed in specific prey carcass sizes, experiments analyzing tooth mark dimensions should consider the influence that carcass size has on the way carnivores modify them. A clear example of this is that Delaney-Rivera et al. (2009) document a significantly smaller range of tooth mark dimensions both in dogs and lions (probably because they were fed on goat limbs) compared to the tooth mark size ranges documented by

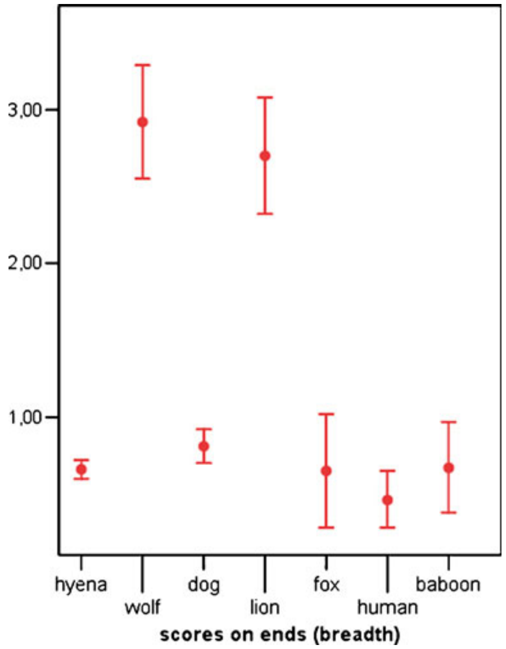

Fig. 6 Mean values and 95 % confidence intervals of tooth score breadth (millimeters) on cancellous ends. They were calculated using the *t* distribution, where *t*·0.025 is the critical value of *t* with *n*−1 degrees of freedom

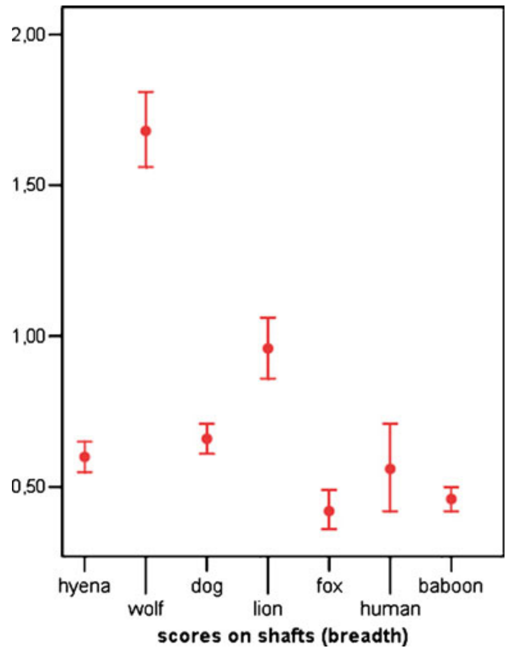

Fig. 7 Mean values and 95 % confidence intervals of tooth score breadth (millimeters) on dense cortical shafts. They were calculated using the *t* distribution, where *t*·0.025 is the critical value of *t* with $n-1$ degrees of freedom

Selvaggio and Wilder (2001), by Dominguez-Rodrigo and Piqueras (2003), and by the present study, where these carnivores fed on larger carcasses, which is the most common carcass size of their predatory range. Something similar is documented in the present study where two hyena-modified bone sets are used, showing drastically different tooth mark sizes. Although the Eyasi hyena den has been argued to have been modified by pups (see above), the lack of direct observation opens the possibility that such small tooth mark dimensions could also be the result of hyenas (irrespective of their age) feeding on ovicaprids, which is the bulk of the fauna documented at the den (Prendergast and Domínguez-Rodrigo 2008). In sharp contrast, the Maasai Mara den data, based on tooth-marked bones from medium-sized and large carcasses, show a much bigger range of mark dimensions and bigger central values. This brings into question inferences of tooth mark dimension and attribution to carnivore types based on data from small carcasses alone.

Delaney-Rivera et al. (2009) also argued that there was an increase in the correlation of carnivore body size as bone density decreased. This may have also much to do with carcass size, given that with a sample including larger carcasses (this study), the differences of large and small carnivores were ambiguous and no relationship between carnivore size and tooth mark size on cancellous bone was observed.

Delaney-Rivera et al. (2009) argued that the presence of many smaller pit dimension values in their sample was probably due to the inability of other researchers to measure small marks accurately because they did not use the same digital method. The present study does not support this assertion, since small marks were successfully measured using the same methods as in previous studies (e.g., Dominguez-Rodrigo and Piqueras 2003). It should be stressed that much of the ambiguity in discriminating carnivore sizes using tooth pit dimensions came from the observation of Delaney-Rivera et al. (2009) that small-sized carnivores (such as mustelids) could create marks overlapping in size with medium-sized felids. This was already documented by Selvaggio and Wilder (2001) and Dominguez-Rodrigo and Piqueras (2003), who argued that medium-sized felids modify bones in a similar way to smaller carnivores. In addition, Delaney-Rivera et al. (2009) mentioned that lions also created smaller pits than documented by previous researchers, admitting as a possible cause the artificial conditions of the feeding experiment. They argued that large felids were disinterested in bones and that “the high frequency of small pits may reflect their relative satiation on the day they were presented the bones, and thus their lack of motivation to forcefully tooth mark them” (Delaney-Rivera et al. 2009, p. 2602).

Delaney-Rivera et al. (2009) also noticed that score length was dependent on other variables in addition to carnivore size, such as bone type and bone size, and focused on score breadth in their analysis. They documented that “most of the marks above 1 mm in breadth were made by medium and large-sized mammals, including hyenas, bears, African lions, and a dog” (Delaney-Rivera et al. 2009, p. 2602). These results are supported by the present study (Table 2). The only outlier in their analysis was Domínguez-Rodrigo and Piqueras’ (2003) baboon tooth-marked sample, but the addition of a larger number of inconspicuous marks in the present study has significantly reduced the average values for their score dimensions, hence the influence of sample sizes in central values and ranges of variation.

One could argue that the types of teeth (incisors, canines, premolars, and molars) determine variability documented in tooth mark types; however, tooth diversity probably has a minor input in the resulting tooth mark dimensions, when these are evaluated in terms of sample population and not as isolated marks. The reason is that incisors and canines are normally not used for defleshing bulk meat close to bone, nor for bone-breaking activities, which are the ones more prone to generate the bulk of tooth marks on bone surfaces. Given the overall similarity of premolar and molar cusps, the main active effectors in mark producing, differentiating between these two types of teeth would not be relevant. It could also be argued that tooth dimensions vary if one considers tooth morphology (e.g., secodont versus bunodont taxa). However, when one considers tooth mark sizes reported for secodont carnivores (this study) and bunodont taxa (Dominguez-Rodrigo and Piqueras 2003; Delaney-Rivera et al. 2009; Saladié et al. 2012), differences in tooth mark dimensions show a clearer correlation with carnivore size and not dentition type. Bears, for instance, are more similar to spotted hyenas and lions than they are to smaller bunodont carnivores such as humans (Delaney-Rivera et al. 2009; Saladié et al. 2012). It could equally be argued that the degree of "freshness" of carcasses could influence the size of pits and marks on bone surfaces. However, given that most tooth marking takes place during carcass consumption and this occurs while bones are green, such a variable has not been documented to be of any relevance by any researcher conducting experimental work. The number of predators could also be argued to have an influence on the resulting tooth mark dimensions. Experimental work shows that this is also not a factor since tooth mark sizes are the sole result of the degree of impact of tooth effectors on bone surfaces and that does not depend on how many predators are consuming the carcass. This is justified by looking at tooth mark size distribution when predators are solitary or gregarious and their overlap when carnivore size is considered. For example, bears are solitary carcass consumers and the tooth mark sizes they inflict on bones are similar to those of large carnivores who are more gregarious (Saladié et al. 2012).

What this study has shown is that the two statistically detectable meaningful variables in tooth mark dimensions are carnivore size (small versus large) and carcass size; small carcasses are more ambiguous in enabling us to detect carnivore types because the marks inflicted on them by carnivores (irrespective of their size) show strong overlap. Large carnivores do not need to apply as much strength to tooth mark the small carcasses as they do with larger carcasses. When stressing carnivore size, this applies also to age, as the contrast between the Maasai Mara and the Eyasi dens show. Subadult individuals of the same taxa may generate a different dimensional spectrum of marks compared to adult individuals. Delaney-Rivera et al. (2009) are right when they argue that archeofaunal assemblages may be palimpsests of modifications inflicted by more than one agent, and thus, applying these referential frameworks should be done with caution. This cautionary note should be applied also to referential analogs derived from non-controlled samples, where the number of tooth-marking agents cannot be reliably determined.

Conclusions

The present study has shown that when using large samples of marks, small and large carnivores can be potentially differentiated, provided the mark samples are from natural carcasses that represent the most common carcass sizes consumed by each type of carnivore in the experiment. Differences in tooth mark size are more prominent with tooth marks on dense cortical shafts than with those on spongy ends. These differences are also more perceptible when using tooth pits rather than scores. Previous claims of ambiguity are mostly based on either small tooth mark sample sizes or data from tooth marks on small carcasses. Small carcasses (such as sheep or goats) are marginal in the predatory range of several large carnivores in their natural environments. They are not the type of prey commonly consumed by either lions or hyenas in the wild, other than in game-depleted areas with a high anthropogenic impact in local ecology. This underscores the need to understand tooth marking of each carnivore within their predatory range and the carcass sizes represented in it. This study also calls attention to the effect that experimental conditions have on the outcome of experiments. In the present study, we have used data from carcasses consumed by carnivores in their natural environments (hyenas, lions, wolves, foxes, humans) and under control, and the results show important discordances with previous published work carried out in captivity or under artificial conditions, probably because of some of the reasons described above (Delaney-Rivera et al. 2009).

When using samples of marks, instead of isolated marks, large and small carnivores can be best differentiated, according to the present study, by using tooth pit dimensions (and to a lesser extent tooth score breadth) on shafts. This supports previous studies claiming that differentiating carnivore taxa by using tooth mark dimensions was spurious but also that distinguishing small from large carnivores could be empirically supported (Dominguez-Rodrigo and Piqueras 2003; Delaney-Rivera et al. 2009). It is important to stress that this study (as well as previous research) shows that after a certain threshold (marked by the uppermost size of tooth marks made by small carnivores), breadth and length dimensions can be used on isolated marks to differentiate large from smaller carnivores. We would like to emphasize also that the purported ambiguity of tooth mark dimensions (as reported for small carcasses) could be overcome if this variable is inserted in a multivariate taphonomic approach, considering other taphonomic attributes.

This study supports the claim of Delaney-Rivera et al. (2009) that carnivore attribution of bone modification in any given assemblage ought to be made in combination with other bone modification variables, such as furrowing distribution (Haynes 1980b, 1983; Domínguez-Rodrigo et al., in preparation). Furthermore, it has been argued that twenty-first century taphonomy needs to be built on the wealth of information stemming from multivariate approaches (Domínguez-Rodrigo and Pickering 2010). Therefore, the attribution of modified bone assemblages to specific carnivore types can be heuristically better supported when in conjunction with a larger set of variables, which in their combination create a better supported diagnosis of agency.

Acknowledgments We thank J. Kerbis-Peterhans for having allowed one of us (MDR) access to the Maasai Mara hyena den collection. We thank F. Bárcena for having allowed JY access to the Campelo Montain wolf carcasses and S. Ripoll for carcasses processed by foxes in Ayllón. We are also indebted to two anonymous reviewers for their useful comments on an earlier draft of this paper. We also thank M. Prendergast for her comments and editorial suggestions.

References

Andrews P, Fernández-Jalvo Y (1997) Surface modifications of the Sima de los Huesos fossil humans. J Hum Evol 33:191–217

Binford LR (1981) Bones: ancient men, modern myths. Academic Press, New York

Blumenschine RJ (1986) Early hominid scavenging opportunities. Implications of carcass availability in the Serengueti and Ngorongoro ecosystems. BAR International Series 283. BAR International, Oxford

Blumenschine RJ (1988) An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. J Archaeol Sci 15:483–502

Blumenschine RJ (1995) Percussion marks, tooth marks and the experimental determinations of the timing of hominin and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. J Hum Evol 29:21–51

Borrero LA, Martin FM, Vargas J (2005) Tafonomía de la interacción entre pumas y guanacos en el Parque Nacional Torres del Paine, Chile. Magallania 33:95–114

Brain CK (1981) The hunters or the hunted? University of Chicago Press, Chicago

Bunn HT (1982) Meat-eating and human evolution: studies on the diet and subsistence patterns of Plio-Pleistocene hominins in East Africa. Ph.D. dissertation. University of California, Berkeley

Cavallo JA (1998) A re-examination of Isaac's central-place foraging hypothesis. Ph.D. dissertation, Anthropology Department, Rutgers, New Brunswick, NJ

Cavallo JA, Blumenschine RJ (1989) Tree-stored leopard kills: expanding the hominid scavenging niche. J Hum Evol 18 (4):393–399

Delaney-Rivera C, Plummer TW, Hodgson JA, Forrest F, Hertel F, Oliver JS (2009) Pits and pitfalls: taxonomic variability and patterning in tooth mark dimensions. J Archaeol Sci 36:2597–2608

Domíguez-Rodrigo M (1999a) Flesh availability and bone modification in carcasses consumed by lions. Paleogeography Paleoclimate Paleoecology 149:373–388

Domíguez-Rodrigo M (1999b) Meat-eating and carcass procurement by hominids at the FLK Zinj 22 site, Olduvai Gorge, Tanzania: a new experimental approach to the old hunting-versus-scavenging debate. In: Ullrich H (ed) Lifestyles and survival strategies in Pliocene and Pleistocene hominids. Edition Archea, Schwelm, pp 89–111

Domínguez-Rodrigo M (1993) La formación de las acumulaciones óseas de macrofauna: Revisión de los criterios de discernimiento de los agentes biológicos no antrópicos desde un enfoque ecológico. Zephyrus 46:03–122

Domínguez-Rodrigo M, Martí R (1996) Estudio etnoarqueológico de un campamento temporal Ndorobo (maasai) en Kulalu (Kenia). Trab Prehist 131:131–144

Domínguez-Rodrigo M, Pickering TR (2010) A multivariate approach for discriminating bone accumulations created by spotted hyenas and leopards: harnessing actualistic data from East and Southern Africa. J Taphonomy 8:155–179

Dominguez-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, Serrallonga J, Medina V (1998) Food availability and social stress among captive baboons: referential data for early hominid food transport at sites. l'Anthropologie 36:225–230

Domínguez-Rodrigo M, Barba M, Egeland CP (2007a) Deconstructing Olduvai: a taphonomic study of the Bed I sites. Springer, Dordrecht

Domínguez-Rodrigo M, Egeland CP, Pickering TR (2007b) Equifinality in carnivore tooth marks and the extended concept of archaeological palimpsests: implications for models of passive scavenging of early hominids. In: Pickering TR, Schick K, Toth N (eds) Breathing life into fossils: taphonomic studies in honor of C.K. (Bob) Brain. Stone Age Institute Press, Bloomington, pp 255–288

Estévez EJ, Mamelli L (2000) Muerte en el canal: experiencias bioestratigráficas controladas sobre la acción sustractiva de cánidos. Archaeofauna 9:7–16

Faith JT (2007) Sources of variation in carnivore tooth-marks frequencies in a modern spotted hyena (*Crocuta crocuta*) den assemblage, Amboseli Park, Kenya. J Archaeol Sci 34(10):1601–1609

Fernández-Jalvo Y, Andrews P (2011) When humans chew bones. J Hum Evol 60:117–123

Hair JF, Anderson RE, Tatham RL, Black WC (1998) Multivariate data analysis. Prentice Hall, New York

Haynes G (1980a) Prey bones and predators. Potential ecologic information from analysis bones of bone site. Ossa 7:75–97

Haynes G (1980b) Evidence of carnivore gnawing on Pleistocene and recent mammalian bones. Paleobiology 6(3):341–351

Haynes G (1982) Utilization and skeletal disturbances of north American prey carcasses. Artic 35:266–281

Haynes G (1983) A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. Paleobiology 9:164–172

Kerbis-Peterhans JC (1990) The role of porcupines, leopards and hyaenas in ungulate carcass dispersal: implications for paleoanthropology. Department of Anthropology, University of Chicago, Chicago

Lewis JP, Traill A (1999) Statistics explained. Addison-Wesley, Harlow

Lloveras L, Moreno-García M, Nadal J (2008) Taphonomic analysis of leporid remains obtained from modern Iberian Lynx (*Lynx pardinus*) scats. J Archaeol Sci 35:1–13

Mondini M (2000) Tafonomía de abrigos rocosos de la Puna. Formación de conjuntos escatológicos por zorros y sus implicaciones arqueológicas. Archeofauna 9:151–164

Montalvo CI, Pessino ME, Bagatto FC, Montalvo CI (2008) Taphonomy of the bones of rodents consumed by Andean hog-nosed skunks (*Conepatus chinga*, Carnivora, Mephitidae) in central Argentina. J Archaeol Sci 35:1481–1488

Muñoz AS, Mondini M, Durán V, Gasco A (2008) Los pumas (*Puma concolor*) como agentes tafonómicos. Análisis actualístico de un sitio de matanza en los Andes de Mendoza, Argentina. Geobios 41:123–131

Nasti A (1996) Predadores, carroñeros y huesos: la acción del puma y el zorro como agentes modificadores de esqueletos de ungulados en la Puna meridional, Argentina. In: Meléndez Hevia G, Blasco Sancho MF, Pérez Urresti I (eds) II Reunión de Tafonomía y Fosilización. Zaragoza, pp 265–269

Pickering TR, Dominguez-Rodrigo M, Egeland CP, Brain CK (2004) Beyond leopards: tooth marks and the contribution of multiple carnivore taxa to the accumulation of the Swartkans Member 3 fossil assemblage. J Hum Evol 46:595–604

Pinto-Llona AC, Andrews PJ, Etxebarría F (2005) Tafonomía y Paleobiología de úrsidos cuaternarios cantábricos. Fundación oso de Asturias, Proaza

Prendergast ME, Domínguez-Rodrigo M (2008) Taphonomic analyses of a hyena den and a natural-death assemblage near Lake Eyasi (Tanzania). J Taphonomy 6(3–4):301–335

Ruiter JD, Berger LR (2000) Leopard as a taphonomic agents in dolomitic caves. Implications for bone accumulations in the hominid bearing deposits of South Africa. J Archaeol Sci 27:665–684

Saladié P, Huguet R, C Díez, Rodríguez-Hidalgo A, Carbonell E (2012) Taphonomic modifications produced by modern brown bears (*Ursus arctos*). Int J Osteoarchaeol (in press)

Selvaggio MM (1994) Identifying the timing and sequence of hominid and carnivore involvement with Plio-Pleistocene bone assemblages from carnivore tooth marks and stone-tool butchery marks on bone surfaces. Ph.D. dissertation, Rutgers University, New Brunswick

Selvaggio MM, Wilder J (2001) Identifying the involvement of multiple carnivore taxon with archaeological bone assemblages. J Archaeol Sci 28:465–470

Sutcliffe AJ (1973) Caves of the east African Rift Valley. Trans Cave Res Group Great Brit 15:41–65

Wilcox RR (2005) Introduction to robust estimation and hypothesis testing. Elsevier Academic Press, London

Yravedra J, Lagos L, Bárcena F (2011) A taphonomic study of wild wolf (*Canis lupus*) modification of horse bones in northwestern Spain. J Taphonomy 9:37–66