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Sources of variation in carnivore tooth-mark frequencies in a modern spotted hyena (*Crocuta crocuta*) den assemblage, Amboseli Park, Kenya

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Abstract

Distributions and frequencies of carnivore tooth-marks on large mammal long-bone fragments are commonly used to infer the timing of hominin and carnivore access to prey resources in archaeofaunal assemblages. The strength of these inferences, however, is limited by a broad and currently inexplicable range of tooth-mark frequencies across experimental and archaeological assemblages. Controlling for this variation first requires that the sources be identified. Several sources of variation are examined here in an analysis of tooth-marked bone recovered from a modern spotted hyena (*Crocuta crocuta*) den assemblage in Amboseli Park, Kenya. Results indicate that tooth-mark frequencies: (1) depend on fragment size, (2) vary across mammals of different size classes, (3) are highly variable across equivalent portions of different long-bone elements, and (4) on certain long-bone portions are correlated with bone density and can be depressed in archaeological assemblages subjected to density-mediated attrition. Stronger inferences based on tooth-mark frequencies will require that such variation be taken into consideration, and methods for doing so are suggested.
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1. Introduction

Assessing the contribution of hominin and carnivore agents to the formation of archaeological bone assemblages has become increasingly important in zooarchaeological analyses (Assefa, 2006; Binford, 1981; Binford et al., 1988; Blumenschine, 1986, 1988, 1995; Blumenschine and Marean, 1993; Capaldo, 1997, 1998; Domínguez-Rodrigo, 1997; Faith and Behrensmeyer, 2006; Marean et al., 2000; Marean and Kim, 1998; Monahan, 1996; Potts, 1988; Selvaggio, 1998). An understanding of this issue is critical if faunal analysts wish to infer early human carcass-acquisition strategies and, by extension, the role of carnivory in human evolutionary history.

Specifically, much attention has been directed at determining whether early humans had primary access to fully fleshed carcasses, via either a hunting or aggressive scavenging strategy (Bunn, 2001; Bunn and Ezzo, 1993; Bunn and Kroll, 1986; O'Connell et al., 2002), or secondary access to carcass remains defleshed by carnivores, as in a passive scavenging strategy (Binford, 1981).

Attempts to resolve this issue have focused largely on the frequencies and distributions of bone surface modifications (i.e., carnivore tooth-marks, cut marks, percussion marks) on long-bone fragments (Assefa, 2006; Blumenschine, 1995; Blumenschine and Marean, 1993; Capaldo, 1995, 1997, 1998; Domínguez-Rodrigo, 1997, 2002; Domínguez-Rodrigo and Barba, 2006; Marean et al., 2000; Marean and Kim, 1998; Selvaggio, 1994a,b, 1998). Typically, patterns in the archaeological record are compared to results from experimental studies that simulate various scenarios of human and carnivore

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involvement with bone assemblages; these studies include observations in both naturalistic (e.g., Blumenschine, 1988; Capaldo, 1995; Selvaggio, 1994b) and ethnoarchaeological settings (Lupo and O'Connell, 2002). Results from experimental assemblages indicate that carnivore tooth-mark frequencies are particularly sensitive to whether humans or carnivores had primary access to a carcass (Blumenschine, 1995; Capaldo, 1997; Marean et al., 2000; Marean and Kim, 1998; Selvaggio, 1998). When humans precede carnivores in processing a carcass, carnivore tooth-mark frequencies on long-bone mid-shafts are low, presumably because mid-shafts have no appeal to carnivore consumers once they are stripped of meat and marrow. Alternatively, when carnivores are the initial consumers, mid-shafts accumulate elevated frequencies of tooth-marks as a result of carnivores defleshing the bone and breaking open the diaphysis to acquire marrow (Blumenschine, 1988). Despite these generalizations, tooth-mark frequencies vary widely across experimental control samples in which the order of consumer access is constant (Fig. 1). Noting this variation as well as inconsistencies between experimental patterns and those observed in the Plio-Pleistocene archaeological record, Lupo and O'Connell (2002) have suggested that the range of tooth-mark frequencies relative to carcasses condition and the order of consumer access may be very broad and only partially sampled by the current experimental assemblages.

Lupo and O'Connell's (2002) study marks the beginning of a recent trend in which the value of bone surface modification as indicators of behavioral patterns has been seriously questioned (Lyman, 1995, 2005; Pickering and Egeland, 2006). Doubts surrounding the usefulness of bone surface modifications stem from a large and currently inexplicable range of variation across experimental and archaeological assemblages (Lupo and O'Connell, 2002; Lyman, 2005). It is clear that unless the sources of variability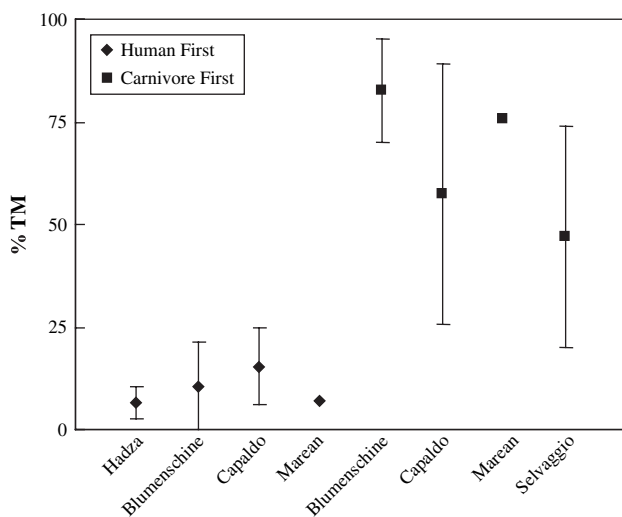 can be identified and corrected for in our analytical frameworks, bone surface damage patterns will continue to be problematic as indicators of the timing and impact of human and carnivore agents on archaeological bone assemblages. If we are to make confident inferences based on tooth-mark frequencies, the first challenge is to identify the sources of variation. In this study, my goal is to examine several potential sources of variation that impact frequencies and distributions of carnivore tooth-marks on the mammal remains recovered from a modern spotted hyena (*Crocuta crocuta*) den in Amboseli Park, southern Kenya (Fig. 2) (Hill, 1981, 1983, 1989).

I consider the following questions of the Amboseli hyena den assemblage: (1) How does long-bone fragment size impact tooth-mark frequencies? (2) How do tooth-mark frequencies vary across taxa of different body size classes? (3) How does the incidence of tooth-marking vary across portions of different long-bone elements? (4) What is the relationship between tooth-mark frequency and bone density? Exploration of these questions is important if we are to identify and ultimately correct for the sources of variation that confound analyses of tooth-mark frequencies in archaeological bone assemblages.

2. The Amboseli Airstrip Den assemblage

The Amboseli Airstrip Den is located in the open grasslands habitat of Amboseli National Park in southern Kenya (Fig. 2). It has been used as a natal and communal den for many generations of spotted hyenas and continues to be active (Behrensmeyer, 1993; Lansing and Behrensmeyer, 2005). The

Fig. 1. Percentage of tooth-marked (% TM) long-bone mid-shaft fragments (mean ± 1 standard deviation, i.e., 68% confidence interval) from ethnographic observations of the Hadza (Lupo and O'Connell, 2002) and experimental carnivore-first and human-first/carnivore-second assemblages (Blumenschine, 1995; Capaldo, 1995; Marean et al., 2000; Selvaggio, 1994b). Data are from Lupo and O'Connell (2002: Table 10).
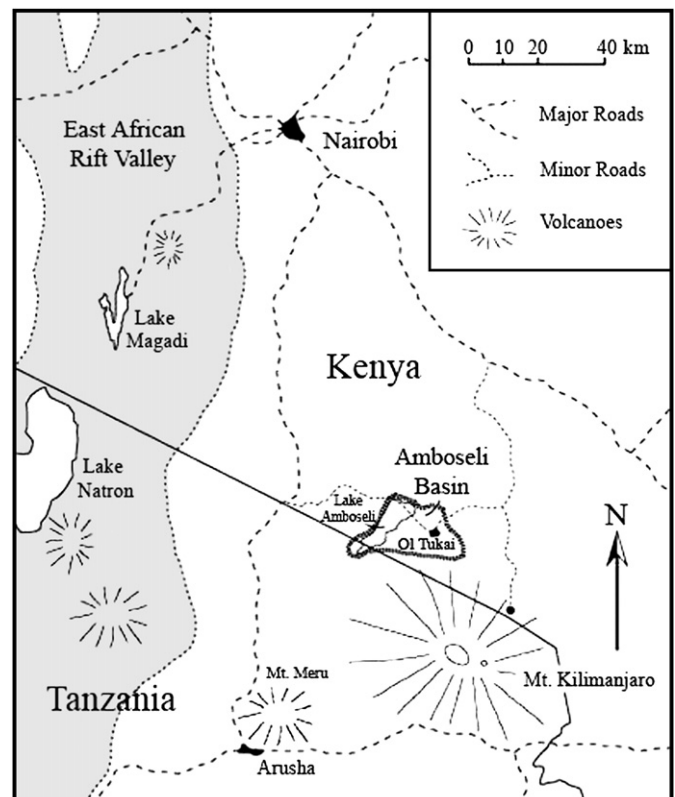

Fig. 2. The location of the Amboseli Basin. Modified from Faith and Behrensmeyer, 2006.

den is a 20 × 4 m open trench resulting from a natural break or partial collapse of calcrete duricrust with numerous small covered passages and underground burrows associated with the low (30–40 cm) walls of the trench (Fig. 3). Spotted hyenas are known to have occupied the den periodically over several decades leading up to 1975, with infrequent occupation between 1969 and 1975 (Faith and Behrensmeyer, 2006). All surface bones visible within the trench were mapped and collected by Andrew Hill in 1975, providing a sample of over 1600 specimens (Hill, 1983, 1989). Excavation was not permitted as the den was then occupied by a group of 15 spotted hyenas (Hill, 1983). It is possible that some small shaft fragments were not recovered by the surface collection as they have been observed to readily penetrate the sediment surface (Gifford-Gonzalez et al., 1985). Even though this is the case, the patterns to be presented here are so robust that it seems unlikely that complete recovery of very small bone fragments would have made any significant difference in the results.

The Airstrip Den bone collection is stored in the Paleontology Department of the National Museum of Kenya (NMK), and with the permission of A. Hill and NMK Paleontology staff, I was able to study this collection in 2006. Table 1 presents the number of identifiable specimens (NISP) and the minimum number of individuals (MNI) represented for each taxon recovered in the Amboseli hyena den assemblage. Specimens that could only be identified as bovids were classified according to Brain's (1981) size classes; the values reported for these groups do not include specimens that were identified to genus and species. The faunal assemblage is dominated by size 3 (Brain, 1981) ungulates, particularly wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*), followed by smaller Grant's gazelle (*Gazella granti*) and Thomson's gazelle (*Gazella thompsoni*).

3. Methods

The sample examined in this study includes all mammal long-bone specimens within Behrensmeyer's (1978) weathering

Fig. 3. The Amboseli Airstrip Den ca. 1993 with three spotted hyenas in the foreground and another in the middle distance. Many more bones littered the trench in 1975. Photograph: A.K. Behrensmeyer.

Table 1
The number of identified specimens (NISP) and minimum number of individuals (MNI) for each taxon recovered in the Amboseli hyena den assemblage

Taxon	NISP	MNI
Connochaetes taurinus	315	16
Equus burchelli	154	12
Gazella granti	41	5
Gazella thompsoni	22	3
Bos taurus	20	3
Equus asinus	5	2
Crocuta crocuta	5	1
Canis cf. *mesomelas*	4	1
Felis caracal	4	1
Pedetes sp.	4	1
Tragelaphus scriptus	3	1
Panthera pardus	2	1
Phacochoerus aethiopicus	2	1
Caprovine	1	1
Panthera leo	1	1
Syncerus caffer	1	1
Aepyceros melampus	1	1
Bovid Size 1	8	1
Bovid Size 2	181	5
Bovid Size 3	139	5
Total	913	63

stages (WS) 0–1 (NISP = 732). Restricting the sample to this subset ensures that tooth-marks are not obscured or obliterated by flaking or extensive cracking of the outer bone surface, thus allowing consistent identification of the marks. When possible, the following information was collected for each long-bone fragment: taxon, taxon size following Brain (1981), element, long-bone portion(s) after Marean and Spencer (1991), maximum length, and presence/absence and location(s) of tooth-marks. Laboratory protocol for the identification of tooth-marks follow the guidelines outlined by Blumenschine (1996). All long-bone specimens were examined for tooth-marks under strong incident light with the aid of a 14 power hand lens.

In quantifying tooth-mark frequencies, the methodology implemented in many published analyses first classifies a specimen according to specific fragment types (e.g., Assefa, 2006; Blumenschine, 1988, 1995; Capaldo, 1997; Domínguez-Rodrigo and Barba, 2006; Marean and Kim, 1998; Monahan, 1996). Following Blumenschine (1988, 1995) these fragment types include epiphyseal fragments, which retain some portion of an articular end, near-epiphyseal fragments, equivalent to Marean and Spencer's (1991) proximal and distal shafts, and mid-shaft fragments, which lack cancellous bone on the medullary surface. For each fragment type, the number of tooth-marked specimens is calculated relative to the total number of specimens within that particular fragment category. In grouping specimens from different elements into fragment types, analysts make the implicit assumption that there is no variation in tooth-mark frequencies across long-bone portions of different elements. Since my goal here is to examine variation across elements *and* portions, a different protocol for tooth-mark quantification is required. First a specimen is classified according to long-bone element and portion(s) following Marean and Spencer's (1991) divisions: proximal

end, proximal shaft, middle shaft, distal shaft, and distal end. Tooth-marks are noted as either present or absent on the portions represented by a given specimen. For example, consider a long-bone fragment that retains part of the proximal end, proximal shaft, and middle shaft and bears tooth-marks on the proximal shaft and middle shaft. Following Blumenschine's system (Blumenschine, 1988, 1995) this specimen would contribute to the number of tooth-marked epiphyseal fragments. According to the system implemented here, this specimen would add to the number of tooth-marked proximal shafts and middle-shafts of a particular skeletal element. These procedures are in agreement with recent arguments for increased specificity in documenting the location of bone surface modifications (Domínguez-Rodrigo, 1997, 2002).

In the following analyses, tooth-marks are often discussed in terms of the number of marked specimens or portions relative to the total number of specimens or portions under consideration. The percentage of tooth-marked (% TM) specimens refers to the number of tooth-marked specimens in a given class of specimens (e.g., all size 3 mammal specimens, all tibia mid-shafts) relative to the total number specimens within that class.

4. Results

4.1. Relationship between long-bone fragment size and tooth-mark frequency

The probability that any given specimen will display a tooth-mark is partially a function of the size and surface area of that specimen (Pobiner et al., 2002). Here, maximum length is used to represent specimen size. The % TM for long-bone specimens divided into arbitrary 20-mm class intervals are provided in Table 2. Across different size classes, % TM ranges from 14.3% to 94.8%. The correlation between % TM and maximum specimen length is positive and significant ($r_s = 0.786$, $p = 0.021$). Thus, longer specimens are more likely to be tooth-marked.

4.2. Tooth-mark frequencies across body size classes

The experimental assemblages used to interpret archaeological tooth-mark frequencies are composed primarily of size 2 or size 3 bovids (e.g., Blumenschine, 1988, 1995; Blumenschine and Marean, 1993; Capaldo, 1995, 1997; Marean and Kim, 1998; Selvaggio, 1994b, 1998). Most analysts compare their archaeological data to these actualistic assemblages without adequate consideration of errors introduced by taxonomic variation, which may result from body size or morphological differences across species (e.g., Assefa, 2006; Lupo and O'Connell, 2002; Marean et al., 2000; Marean and Kim, 1998; Monahan, 1996; Selvaggio, 1998). Table 3 presents the % TM across mid-shaft fragments of size 2 and size 3 mammals. To control for variation in tooth-mark frequencies relating to differential destruction of long-bone epiphyses and near-epiphyses between size classes (see Faith and Behrensmeyer, 2006) the sample must be restricted to long-bone mid-shafts. As body size increases, there is a marked increase (11.8%) in the frequency of tooth-marked long-bone mid-shafts. A chi-square test indicates that this difference is significant ($\chi^2 = 6.53$, $p = 0.011$). However, given the positive relationship between long-bone fragment length and tooth-mark frequency, the increase in % TM across body size classes may simply reflect variation in long-bone fragment size. Indeed, the mean fragment length attributed to size 3 bovids is 64.1 mm compared to 45.1 mm for size 2 bovids. This difference is highly significant ($t = 7.29$, $p < 0.001$). To overcome the influence of fragment size on tooth-mark frequencies, a comparison of similar sized fragments is necessary. This is illustrated in Table 3 with a comparison of size 2 and 3 mid-shaft fragments with maximum lengths between 20.0 and 60.0 mm. Within this subset, mean fragment lengths are indistinguishable (size 2 mean 37.4 mm, size 3 mean 38.9 mm, $t = -0.970$, $p = 0.333$). With the correction for long-bone fragment size, only a slight (1.3%) non-significant ($\chi^2 = 0.04$, $p = 0.851$) difference in tooth-mark frequencies is apparent.

4.3. Tooth-mark frequencies across long-bone elements and portions

Variability in tooth-mark frequencies in different long-bone elements and portions are examined using chi-square tests and adjusted residuals (see Grayson and Delpech, 2003). The adjusted residuals are used to examine how observed frequencies of tooth-marks differ from expected frequencies; they are to be read as standard normal deviated (Everitt, 1977). The sample examined here includes long-bones of size 2 and 3 mammals. Metacarpals and metatarsals are reported as metapodials since

Table 2
The percentage of tooth-marked (% TM) long-bone fragments across 20 mm class intervals

Maximum length (mm)	N	% TM
0–20.0	21	14.3
20.1–40.0	196	45.9
40.1–60.0	170	71.8
60.1–80.0	130	83.8
80.1–100.0	77	94.8
100.1–120.0	42	92.9
120.1–140.0	18	94.4
>140.1	78	85.9
Total	732	71.0

Table 3
% TM for all long-bone mid-shafts of size 2 and 3 mammals and for long-bone mid-shafts with maximum lengths between 20.0 and 60.0 mm

	N	% TM
Long-bone mid-shafts		
Size 2	238	63.4
Size 3	174	75.3
Long-bone mid-shafts		
(fragment length 20.0–60.0 mm)		
Size 2	175	57.7
Size 3	78	59.0

many specimens could only be identified as such. As illustrated in Table 4, there are highly significant differences in the incidence of tooth-marks across portions of different elements ($\chi^2 = 33.46$, $p = 0.006$). The distribution of expected values within this table meets all contingency table sample size requirements (Siegel, 1956; Zar, 1999). The adjusted residuals highlight an abundance of tooth-marked tibia proximal shafts, humerus distal shafts and distal ends, and radius mid-shafts, as well as a paucity of tooth-marked humerus mid-shafts. In this bone assemblage, tooth-marks are not distributed equivalently across portions of different long-bone elements.

Examination of the range in % TM across similar portions of different elements also reveals important differences. As indicated in Table 4, the % TM for long-bone epiphyses ranges from 15.4% to 100% across all elements. For proximal/distal shaft portions, the range is less extreme although still quite broad at 45.8% to 75.0%. In contrast, long-bone middle-shafts provide a relatively consistent pattern with a range between 71.6% and 82.4%.

4.4. Relationship between bone density and tooth-mark frequency

It has been well documented that carnivore destruction of bone is a density-mediated process (Brain, 1981; Lam et al., 1998; Marean and Spencer, 1991; Marean et al., 1992). Given that any quantitative assessment of tooth-mark frequency on bone is partially dependent on the degree of bone destruction, a relationship between % TM of different long-bone portions and bone density is likely. For example, we might expect elevated frequencies of tooth-marks on denser portions that are difficult to consume, such as limb shafts. Alternatively, there could be more tooth-marks on the lower density epiphyseal or near-epiphyseal portions because of increased carnivore interest in these portions. Here, I examine the relationship between % TM and bone density separately for proximal and distal epiphyses, proximal and distal shafts, and mid-shafts using Spearman's rank-order correlation coefficient. Bone density values are those of wildebeest as determined by Lam et al. (1999). In the analysis of the shaft portions, metacarpals and metatarsals are combined; in these cases the bone density values of metacarpals and metatarsals are averaged.

Relationships between % TM (from Table 4) and bone density are plotted in Figs. 4–6. For epiphyses, a significant negative correlation between % TM and bone density is apparent ($r_s = -0.655$, $p = 0.021$), such that the more dense portions yield the lowest % TM (Fig. 4). There is a moderate negative relationship between % TM and bone density of proximal and distal long-bone shafts (Fig. 5; $r_s = -0.551$, $p = 0.098$). In contrast, the correlation between % TM and bone density for mid-shafts is positive and non-significant (Fig. 6; $r_s = 0.600$, $p = 0.284$).

5. Discussion

Analysis of the Amboseli Airstrip Den long-bone sample provides unambiguous evidence for a positive relationship between long-bone fragment length and % TM. Such a pattern is expected because the likelihood of a specimen displaying positive evidence of tooth-marks is proportional to its surface area (Pobiner et al., 2002). This implies that all the processes affecting fragment size in a bone assemblage, in addition to carnivore activity, e.g., trampling, sediment compaction and subaerial weathering, can drive down the observed % TM. This, in turn, calls into question direct comparisons of experimental assemblages subjected to only one or two taphonomic agents (i.e., humans and carnivores) and archaeofaunal assemblages that have been subjected to multiple destructive processes. Other researchers have noted that long-bone fragmentation can impact frequencies of bone-surface modifications (e.g., Blumenschine, 1995; Capaldo, 1995, 1997; Lupo and O'Connell, 2002; Marean et al., 2000), although attempts to correct for this problem are rare. Marean et al. (2000) have taken an important step towards resolving this issue by removing fragments with fracture patterns characteristic of dry-bone breakage from their analytical sample following the guidelines developed by Villa and Mahieu (1991). To ensure comparability between experimental and archaeological bone assemblages, future efforts would benefit from enhanced tools for identifying dry-bone breakage patterns and from quantitative comparisons of long-bone shaft fragment size.

The impact of long-bone fragment length on % TM is also well illustrated by the analysis of tooth-mark frequencies of size 2 and 3 mammals. Initial comparisons between the two size groups indicated that size 3 mammals accumulate

Table 4
Tooth-mark (TM) frequencies, percentages (in parentheses), and adjusted residuals (AR) across all long-bone elements and portions

| Portion	Element									
	Femur		Tibia		Humerus		Radius		Metapodials	
	TM	AR	TM	AR	TM	AR	TM	AR	TM	AR
Proximal end	2 (66.6)	−0.08	6 (60.0)	0.25	3 (100)	−0.49	2 (15.4)	−1.78	15 (34.1)	1.66
Proximal shaft	6 (75.0)	−0.12	24 (68.6)	**2.36***	8 (72.7)	−1.21	13 (48.1)	−1.15	32 (61.5)	−0.05
Middle shaft	14 (82.4)	−1.47	47 (77.0)	−0.06	25 (80.6)	**−2.22***	58 (71.6)	**2.12***	97 (74.0)	0.67
Distal shaft	10 (71.4)	1.55	11 (45.8)	−1.82	20 (64.5)	**2.76****	13 (72.0)	0.11	28 (57.4)	−1.40
Distal end	3 (100)	0.87	3 (20.0)	−0.99	8 (61.5)	**2.71****	3 (33.3)	−1.06	8 (34.8)	−0.72
χ^2	**33.46****									

Significant values are in bold. *$p < 0.05$, **$p < 0.01$.
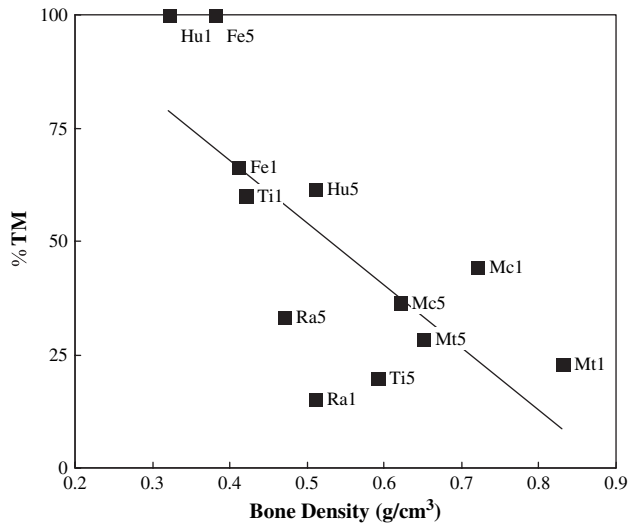
Fig. 4. The relationship between % TM and bone density of wildebeest (Lam et al., 1999) for long-bone epiphyses ($r_s = -0.655$, $p = 0.021$). Fe, femur; Ti, tibia; Mt, metatarsal; Hu, humerus; Ra, radius; Mc, metacarpal; 1, proximal end; 5, distal end.
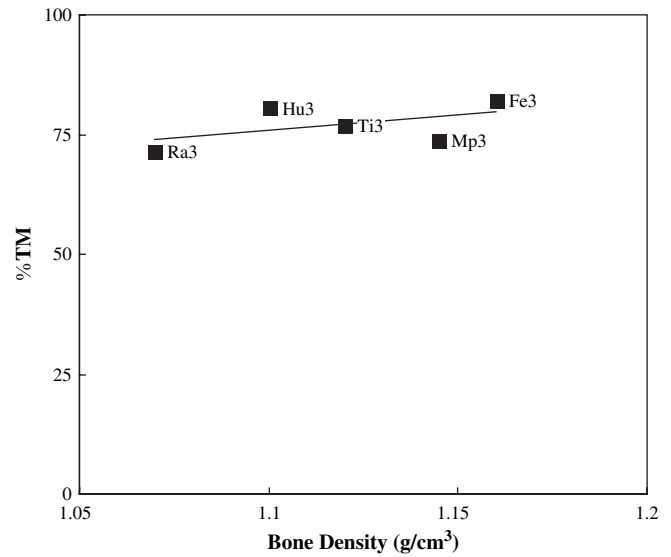

Fig. 6. The relationship between % TM and bone density of wildebeest (Lam et al., 1999) for long-bone mid-shafts ($r_s = 0.600$, $p = 0.284$). Fe, femur; Ti, tibia; Hu, humerus; Ra, radius; Mp, metapodial; 3, middle shaft.

significantly higher frequencies of tooth-marks. The same pattern has been noted previously by Blumenschine and Marean (1993) in a comparison of experimental carnivore-only assemblages. They attribute the elevated incidence of tooth-marks on the larger mammals to their more robust diaphyses. While this may be partially responsible for the patterns they document, analysis of the Amboseli Airstrip Den assemblage indicates that fragment length may be the driving factor behind the differences; tooth-mark frequencies are elevated in larger taxa simply because their bone fragments are longer and more likely to bear evidence of carnivore damage. Once size is taken into account by comparing subsets of size 2 and 3 specimens of equivalent lengths, the significant difference in the incidence of tooth-

marks disappears. Such results are promising with respect to interpreting the fossil record, since one would hope that carcass remains processed by the same agent would bear similar patterns in % TM, regardless of prey body size.

That the taxonomic composition of a faunal assemblage can introduce upwards of a 10% difference in the frequency of tooth-marked specimens represents yet another variable behind the broad range of observed variation in experimental assemblages. For example, Blumenschine's (1988, 1995) experimental assemblages conducted in the Serengeti include mammal remains ranging in size from Thomson's gazelle (*Gazella thompsoni*; size 1) to buffalo (*Syncerus caffer*; size 4), Marean et al.'s (2000) experimental assemblage conducted at the Berkeley Hyena Colony include only sheep (*Ovis aries*; size 2), and Capaldo's (1995, 1997) experimental assemblage includes a range of small (e.g., Grant's gazelle) and medium (e.g., wildebeest) bovids. If long-bone fragment size varies across taxa of different size groups for these assemblages, as in the Amboseli assemblage, it follows that % TM should also display a broad range of variation. This can be remedied by taking long-bone fragment size into account when making comparisons of tooth-mark frequencies across experimental and archaeological assemblages.

Analysis of the Amboseli Airstrip Den assemblage indicates that carnivore tooth-mark frequencies are highly variable across portions of different long-bone elements. With the exception of middle-shafts, there is a broad range in % TM across the portions of different elements. Thus, overall tooth-mark frequencies in a bone assemblage are influenced by the particular combination of elements represented at a site. This is shaped by differential transport of elements in addition to differential destruction of these elements and portions (see Faith and Behrensmeyer, 2006). When analyzing carnivore tooth-mark frequencies in modern or fossil assemblages it is clearly important to treat different elements and portions
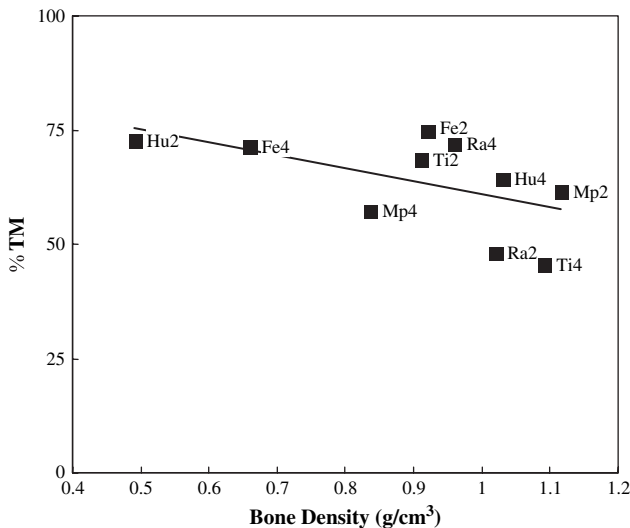

Fig. 5. The relationship between % TM and bone density of wildebeest (Lam et al., 1999) for long-bone proximal and distal shafts ($r_s = -0.551$, $p = 0.098$). Fe, femur; Ti, tibia; Hu, humerus; Ra, radius; Mp, metapodial; 2, proximal shaft; 4, distal shaft.

separately. Nevertheless, the common practice has been to classify specimens according to fragment types without considering the specific element to which the specimen belongs (e.g., Assefa, 2006; Blumenschine, 1995; Capaldo, 1997; Marean and Kim, 1998; Selvaggio, 1998; but see Domínguez-Rodrigo and Barba, 2006). These methods are prone to error resulting from inter-element differences in % TM; results will vary according to the representation of elements and portions in an assemblage. The consistency in % TM across the mid-shafts of all elements suggests that this is the only long-bone portion for which "element-blind" combinations of specimens could be justified. This is fortunate, as it has been noted that mid-shafts provide the clearest distinction between carnivore-first and hominid-first assemblages (Blumenschine, 1988; Marean et al., 2000; Marean and Kim, 1998).

The relationship between % TM and bone density for different long-bone portions can also contribute to inconsistencies between experimental assemblages and archaeological bone assemblages. The % TM of long-bone epiphyses shows a strong negative correlation with bone density. A similar, but weaker, correlation is also evident for long-bone proximal/distal shafts. Because carnivores selectively consume the lowest density long-bone portions (Marean and Spencer, 1991; Marean et al., 1992), it is no surprise that the surviving fragments of these preferred portions will accumulate relatively more tooth-marks. Given that this pattern is related to carnivore behavior, it follows that this relationship should hold for other carnivore-modified assemblages. This relationship has serious implications for archaeological assemblages where density-mediated attrition has altered the frequency of long-bone portions (Grayson, 1989; Lyman, 1984, 1985, 1994). Density-mediated destruction can selectively remove the subset of specimens that retain the highest % TM, thereby depressing the observed percentages of tooth-marked epiphyses and proximal/distal shafts. Only middle-shaft fragments, which show no relationship with bone density, will accurately reflect original % TM.

The sources of variation in carnivore tooth-mark frequencies identified in this study can be explained by a combination of carnivore behavior and the physical characteristics of bone (e.g., fragment length, element/portion, density). Since these variables should transcend specific carnivores and their bone accumulations, it follows that they have the potential to confound analyses of tooth-mark frequencies in other types of bone assemblages (e.g., archaeological assemblages), modified by a range of bone-crunching carnivores.

5.1. Correcting for the variation

Accounting for the sources of variation in carnivore tooth-mark frequencies across actualistic and archaeological assemblages is necessary if faunal analysts are to use these frequencies as indicators of past behavior. The analyses presented above support Lupo and O'Connell's (2002) suggestions that interpreting tooth-mark frequencies is a far more complex task than previously imagined. However, for all factors identified here, steps can be taken to overcome these problems and enhance the resolution of tooth-mark analyses:

(1) *Correct for differences in bone fragment length*. Meaningful comparisons between actualistic and archaeological bone assemblages require that tooth-mark frequencies are not skewed by differences in long-bone fragment length. This factor likely contributes to a large degree of the observed variation between actualistic assemblages composed of mammals of different size classes and to inconsistencies between experimental assemblages and archaeological assemblages where dry-bone breakage has reduced fragment lengths. Errors of this sort can be controlled for by comparing subsets of the data that are similar in overall fragment length.

(2) *Analyze specimens according to both long-bone element and portion*. Results presented here indicate that carnivore tooth-mark frequencies are highly variable across different long-bone elements and portions thereof. By combining separate long-bone elements into one analytical sample, tooth-mark frequencies will vary according to the particular combination of long-bone portions represented. Thus, tooth-mark frequencies in archaeological contexts will be influenced by differential transportation and destruction of bone. To overcome this source of error, long-bone specimens should be analyzed separately according to their respective elements (as in Domínguez-Rodrigo and Barba, 2006). Long-bone middle-shafts appear to be the only portion with low levels of error between elements and in this case, grouping different elements into one sample may not introduce error.

(3) *Control for the impact of density-mediated destruction on the representation of epiphyses and near-epiphyses*. The % TM of epiphyses and near-epiphyses display a negative correlation with bone density; the lowest density portions retain the highest % TM. In examining tooth-mark frequencies on these portions, it is important to show that these frequencies haven't been depressed as a result of to density-mediated destructive processes other than carnivore modification (e.g., trampling, chemical leaching (Lyman, 1994)). Current methods for identifying density-mediated attrition (i.e., examining the correlation between bone abundance and bone density) will not suffice since carnivore-modified bone assemblages are likely to display positive correlations between skeletal element representation and bone density (Lam et al., 1998; Marean and Spencer, 1991; Marean et al., 1992). In light of this complication, it is best to consider only the high-density (Lam et al., 1998, 1999) long-bone mid-shafts, which show no correlation between % TM and bone density.

Correcting for the variation in carnivore tooth-mark frequencies will add a new level of complexity to studies focusing on this signal of past behavior. It will also require new examinations of the current body of actualistic bone assemblages. Unless such steps are taken, however, the interpretive power of tooth-mark frequency analyses will remain limited. Based on the above suggestions, errors could be reduced by focusing on long-bone mid-shafts of specimens of comparable sizes.

6. Conclusions

Interpretations of the timing of hominin access to carcass remains and the relative contribution of carnivore and hominin agents to the formation of archaeological bone assemblages rely heavily on the frequencies and distributions of carnivore tooth-marks on long-bone fragments. As a result of a large range of variation in experimental and archaeological bone assemblages, the usefulness of the study of carnivore tooth-marks, as well as other bone surface modifications, has been questioned (Lupo and O'Connell, 2002; Lyman, 2005; Pickering and Egeland, 2006). Using a well-documented modern spotted hyena den assemblage, this paper identifies some previously unexplored sources of variation and suggests methods for overcoming the errors introduced by these variables.

Results of this study provide evidence for a suite of variables that confound comparisons of carnivore-tooth mark frequencies across experimental and archaeological bone assemblages. These variables include: (1) the relationship between long-bone fragment length and % TM, (2) differences in long-bone fragment length across body size classes (3) inter-element differences in carnivore tooth-mark frequencies across long-bone portions, and (4) the relationship between % TM and bone density of long-bone epiphyses and near-epiphyses. The identification of these sources of variation confirm suggestions that the patterns of carnivore-tooth marks are far more complex than previously considered (Lupo and O'Connell, 2002). However, by taking these variables into account and modifying analytical frameworks, it is possible to correct for the error introduced by all variables identified in this study. Caution still must be exercised as these factors certainly do not represent the entire range of variables that contribute to variation in tooth-mark frequencies. Future research is necessary to identify additional sources of variation and develop methods to overcome them.

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