Journal of Archaeological Science (2001) **28**, 465–470
doi:10.1006/jasc.2000.0557, available online at http://www.idealibrary.com on IDEAL®

Identifying the Involvement of Multiple Carnivore Taxa with Archaeological Bone Assemblages

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(*Received 20 November 1999, revised manuscript accepted 29 February 2000*)

Information on the number of carnivore taxa that were involved with archaeological bone assemblages is pertinent to questions of site formation, hominid and carnivore competition for carcasses and the sequence of hominid and carnivore activity at sites. A majority of early archaeological bone assemblages bear evidence that both hominids and carnivores removed flesh and/or marrow from the bones. Whether flesh specialists (felids) or bone-crunchers (hyaenas), or both, fed upon the carcasses is crucial for deciphering the timing of hominid involvement with the assemblages. Here we present an initial attempt to differentiate the tooth mark signature inflicted on bones by a single carnivore species versus multiple carnivore taxa. Quantitative data on carnivore tooth pits, those resembling a tooth crown or a cusp, are presented for two characteristics: the area of the marks in millimetres, and the shape as determined by the ratio of the major axis to the minor axis of the mark. Tooth pits from bones modified by extant East African carnivores and latex impressions of tooth pits from extinct carnivore species are compared to those in the FLK *Zinjanthropus* bone assemblage. Data on tooth mark shape indicate greater variability in the *Zinj* sample than is exhibited by any individual extant or extinct carnivore species in the comparative sample. Data on tooth mark area demonstrate that bone density is related to the size of marks. Taken together, these data support the inference that felids defleshed bones in the *Zinj* assemblage and that hyaenas had final access to any grease or tissues that remained.

Keywords: CARNIVORE TOOTH MARKS, METHODOLOGY, SITE FORMATION, TAPHONOMY.

Introduction

While carnivore gnaw damage is well documented at many early archaeological sites, the identity and number of carnivore taxa that fed on the bones remains elusive (e.g., Leakey, 1971; Binford, 1981; Potts & Shipman, 1981; Shipman, 1983; Bunn & Kroll, 1986; Potts, 1988; Blumenschine, 1995). This problem is compounded by the large number of carnivore taxa that could have inflicted marks on archaeological bones. The carnivore guilds present in East Africa during the Plio–Pleistocene include ancestors of extant felids: lions, leopards and cheetahs (Barry, 1987), as well as three extinct felids *Homotherium* and *Megantereon*, commonly known as "true sabertooths", and *Dinofelis* usually referred to as a "false sabertooth" (Leakey, 1976; Anderson & Kurten, 1981). In addition, evidence indicates that the ancestor of the modern spotted hyaena, *Crocuta crocuta*, and possibly the striped hyaena, *Hyaena hyaena*, and *Chasmaporthetes* were present in East Africa during the Plio–Pleistocene (Turner, 1985). Large canids are also present in the East African Plio–Pleistocene fossil record (Turner, 1986). Identifying which carnivores were involved with archaeological bone assemblages is crucial for evaluating models of carcass procurement by hominids.

Identification of the involvement of specific carnivores with early archaeological bone assemblages could provide pivotal evidence for hominids having either early or late access to carcasses. For example, in models in which hominids are presumed to have had late access to carcasses, felids are most often implicated as the initial consumer (e.g., Blumenschine, 1986, 1988; Marean, 1989; Cavallo & Blumenschine, 1989; Selvaggio, 1994*a*, 1998*b*). On the other hand, those who support hominids having early access to carcasses suggest that the conspicuous gnaw damage on many butchery-marked bones indicate that hyaenas ravaged the assemblage after hominids had removed all the flesh and marrow from the bones (e.g., Bunn & Kroll, 1986; Bunn & Ezzo, 1993; Oliver, 1994). However, recent studies on bone survival demonstrate that marks inflicted on midshafts during butchery (Blumenschine,

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1988; Blumenschine & Selvaggio, 1991) or defleshing by carnivores (Selvaggio, 1994*a*, *b*, 1998*a*) are not significantly altered when hyaenas have final access to hammerstone-fragmented bones. Therefore, tooth marks inflicted on long bone shafts during defleshing by felids can survive in the archaeological record even though an assemblage had been ravaged by hyaenas.

The research presented provides a quantitative method for describing and analysing carnivore tooth marks in archaeological assemblages. It differs from previous research of tooth mark morphology in three ways (Horton & Wright, 1981; Haynes, 1983; Rabinovich, 1990). First, the sample is derived from a greater number of carnivore species than earlier studies. Secondly, this study is limited to comparisons of carnivore tooth marks that resemble a crown or a cusp. And thirdly, the sample is stratified to evaluate the impact of bone density on the area of tooth marks.

Methods and Samples

The tooth marks in this sample were selected by their resemblance to undamaged tooth cusps or complete crowns. Such marks are generally described as tooth pits (Binford, 1981). Tooth pits from three sources are compared: (1) those inflicted on long bones by a single species of extant East African carnivore (N=221); (2) tooth pits moulded from bovid long bones in the 1·8 million years of the FLK *Zinjanthropus* assemblage (N=61) and; (3) latex impressions of tooth crowns and cusps from several extinct carnivore species (N=27). Tooth pits in the modern and archaeological samples were randomly drawn with respect to the size of marks and their location on bones. Therefore, it is assumed that tooth marks in these samples represent those inflicted by both anterior and posterior dentition.

The sample from extant carnivores was collected in 1989–1990 from free-ranging species in Tanzania and from captive spotted hyaenas in the colony established at the University of California, Berkeley. With the exception of hyaenas, the sample of tooth pits on bones were inflicted by natural feeding populations which were comprised of individuals of both sexes and various ages. The results, therefore, are not biased by age or sex.

Extinct carnivore species are represented by latex impressions of undamaged cusps and crowns from carnivore dentition in the Omo fossil assemblage. The impressions were made by lightly pressing the crown or a cusp into a flattened disc of "Cuttersil" latex material. An accurate impression of crown/cusp shape was produced, but because of the initial softness of the material, the area of the impression is larger than a similar mark inflicted on bone. Thus, this sample is excluded from comparisons of tooth mark area.

Extant carnivores are represented by 221 tooth pits. The hyaena and leopard samples are the largest with 77 and 67 tooth marks, respectively. Cheetah (35), lion (38) and jackal (4) are less well represented. Differences among the sample result from the number of bones modified by specific carnivores and the degree of which tooth marks in each sample met a standard of minimal extraneous crushing of the perimeter of the mark.

The *Zinjanthropus* sample was collected during a 5-week study in 1989 and 1990 at the National Museum of Kenya, Nairobi, Kenya. Tooth pits were moulded using "Xanthopren", a material that accurately produces a negative impression of a mark on the bone's surface. The methods used to mould bone modifications with this material have been described fully elsewhere (Shipman & Rose, 1983). Since the moulds are an accurate negative impression of marks on a bone's surface, they are appropriate for comparison with tooth pits from the modern bone sample for both area and shape.

An experiment was conducted to determine the accuracy of computer measurements on moulded tooth marks compared to actual tooth marks on bone specimens. A random sample of eight bone specimens was drawn in which tooth marks had been measured by video-imaging. The tooth marks were moulded using the same material used for the *Zinj* sample. Moulds of shallow marks showed more variation between the samples than deep marks. This was due to the dark colour of the moulds and a shadow effect when the image was projected on the video monitor. The shadow made one portion of the mark's perimeter appear slightly distorted. Since different lighting techniques could not remedy this problem, moulds of shallow tooth pits were deleted from the *Zinj* sample presented here. In contrast, the perimeter of tooth pits on bone specimens were usually well defined on the monitor. In the few cases in which the perimeter of the mark was not clearly visible, a lead pencil was used to lightly trace the mark's perimeter. This greatly enhanced the contrast between the edge of the mark and the bone's surface.

Tooth pits from modern carnivores and those in the *Zinj* sample are stratified to control for the impact of bone density on mark area (Table 1). Three different bones densities were distinguished based on their resistance to tooth penetration: cancellous, thinning cortical and cortical bone. Tooth pits inflicted by a single carnivore species on relatively soft cancellous bone are compared to those inflicted on compact cortical bone. Thinning cortical bone is the diaphyseal portion closest to epiphyses where the cortical surface is weakest.

Jaw strength among different carnivore taxa, as well as tooth size can affect the degree to which teeth penetrate bone. However, cancellous bone presents less resistance to tooth pressure than compact cortical bone. Cortical bone becomes thinner near the ends of diaphyses. Here, on bovids, compact bone begins to include cancellous tissue of the epiphyses. Therefore, thinning cortical bone is neither as easily penetrated as cancellous bone nor is it as resistant to tooth penetration as cortical bone nearer the mid-section of the

Table 1. Mean area of tooth marks stratified by bone type

Carnivore	Cortical bone	Thin cortical bone	Cancellous bone
Spotted hyaenas	*N*=47	*N*=15	*N*=15
Mean	2·36	4·98	21·54
S.D.	1·73	4·19	7·79
95% Conf. int.	(1·85–2·87)	(2·65–7·73)	(11·69–31·40)
Cheetahs	*N*=20	*N*=3	*N*=12
Mean	1·43	4·47	3·18
S.D.	0·75	2·03	3·90
95% Conf. int.	(1·08–1·78)	(0·56–9·50)	(0·70–5·65)
Leopards	*N*=29	*N*=6	*N*=32
Mean	2·21	3·23	6·26
S.D.	3·11	2·33	6·83
95% Conf. int.	(1·03–3·40)	(0·79–5·68)	(3·82–8·71)
Lions	*N*=13	*N*=11	*N*=14
Mean	5·48	19·82	17·90
S.D.	4·53	12·64	16·50
95% Conf. int.	(2·75–8·22)	(11·33–28·31)	(8·57–27·22)
Jackals	*N*=4		
Mean	0·26		
S.D.	0·13		
95% Conf. int.	(0·04–0·47)		
FLK *Zinj*	*N*=49	*N*=5	*N*=7
Mean	1·77	1·25	21·34
S.D.	1·61	0·47	19·55
95% Conf. int.	(1·25–2·29)	(0·66–1·84)	(3·26–39·42)

diaphysis. Thus, the category "thinning cortical bone" controls for tooth mark area on the ends of diaphyseal fragments where the cortical surface is weakest. In this sample, tooth marks on cortical bone include those found on hammerstone-generated diaphyseal fragments and any cortical portions of the bone (distinct from thinning cortical portions) that remained attached to epiphyses after hammerstone impact.

Images of individual tooth pits were captured, digitized and stored in a computer using a video camera with a magnifying lens. A calibration routine computed the number of pixels/mm. The software made it possible to use a mouse to trace around the perimeter of the monitor image of a tooth pit, and create a binary (black and white) image of the mark. The software also included algorithms that processed the binary image and computed characteristics relating to the size and shape of the tooth pit (for details see Selvaggio, 1994*a*).

Results

The area of tooth pits on cancellous bone is greater than those on cortical bone among individual extant carnivore species and for the *Zinj* sample (Table 1, Figure 1). The mean area of tooth pits on cancellous bone in the *Zinj* sample is similar to those inflicted by hyaenas and lions.

For cortical bone, the *Zinj* sample is most similar in area to pits inflicted by cheetahs, leopards and spotted hyaenas. Tooth pit area on thinning cortical bone exhibits the greatest variation among the bone types.

When the ratio of the major axis to the minor axis is compared, tooth pits in the FLK *Zinjanthropus* sample are more variable than those produced by any individual modern or extinct carnivore species (Table 2, Figure 2).

Discussion

The data presented on tooth mark area demonstrate that bone density is related to the size of marks. Tooth pit area on thinning cortical bone, where the diaphysis joins the epiphysis, exhibits the greatest variation among the bone types (Table 1). This appears to be related to differences in bone density in this region.

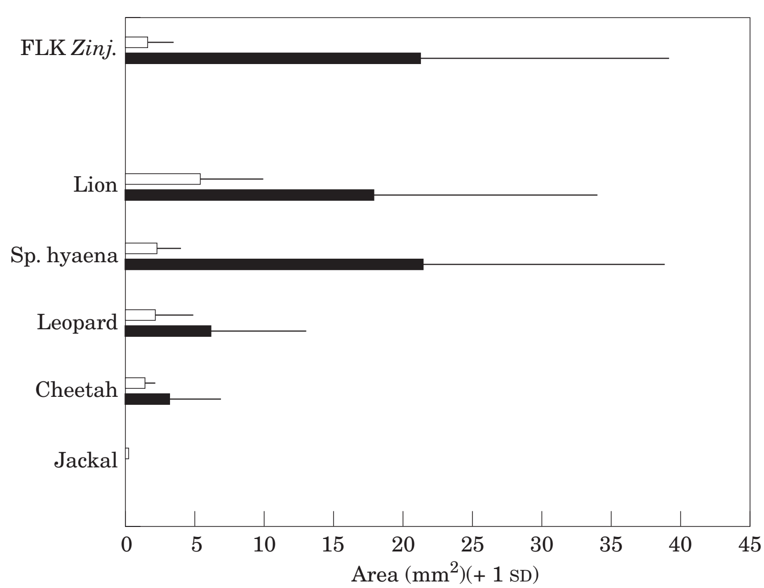

Figure 1. Mean area of tooth pits and one standard deviation. □, cortical bone; ■, cancellous bone.

Table 2. The ratio of the major axis to the minor axis for all tooth marks

Sample	*N*	Mean	± 1 S.D.
FLK *Zinj*	61	2·41	1·83
Dinofelis	3	2·84	0·70
Megantereon	5	1·37	0·14
Percrocuta	8	1·74	0·65
Homotherium	4	2·36	0·50
Extinct felis	7	2·07	0·64
Lion	38	1·75	0·44
Jackal	4	1·55	0·15
Spotted hyaena	77	1·76	0·52
Leopard	67	1·83	0·73
Cheetah	35	1·82	0·49

Tooth pits are larger in area on cancellous bone than on cortical bone for each extant carnivore species (Table 1, Figure 1). The problem of identifying carnivores solely by tooth mark size can be seen in that cheetah tooth pits on cancellous bone are similar in area to those inflicted on cortical bone by hyaenas and leopards. Lion tooth pits on cortical bone are similar in area to leopard tooth pits on cancellous bone. Clearly, bone density and other variables must be considered when inferring the involvement of a specific carnivore species with archaeological bone assemblages.

While both lions and hyaenas inflict tooth marks of similar size on cancellous bone, actualistic research has shown that spotted hyaenas are attracted to the grease in epiphyses even when flesh and marrow have been removed (Blumenschine, 1988; Blumenschine & Selvaggio, 1991; Marean *et al.*, 1992; Selvaggio, 1994*a*, 1998*a*). The involvement of hyaenas at the *Zinj* site is supported by the deletion of a majority of epiphyses from this assemblage. Therefore, the most parsimonious explanation for large-sized tooth marks on cancellous epiphyses is that they were inflicted by hyaenas when they ravaged the assemblage.

The mean area of tooth pits on cortical bone in the *Zinj* sample is most similar to those made by cheetahs, leopards and hyaenas. However, tooth pits in the *Zinjanthropus* sample exhibit more variation in the ratio of the major to the minor axes than those made by any single modern or extinct carnivore species in the sample (Table 2, Figure 2). Therefore, hyaenas can be ruled out as the only carnivore that fed on the carcasses. The great variation in tooth pit shape in the *Zinj* sample indicates more than one carnivore taxon was involved with this assemblage.

Carcasses appear to have been defleshed by medium-sized felids, and hyaenas had final access to any grease or tissues that remained. Many of the bones in this *Zinj* sample bear butchery marks. Therefore, the results support the inference that hominid access was intermediate to carnivore access to bones at this site (Selvaggio, 1994*a*, 1998*a*; Blumenschine, 1995).

Conclusions

Early archaeological bone asemblages are usually multi-patterned by a variety of physical and biological agents. While carnivore damage is often part of the pattern, only one carnivore, the spotted hyaena, has been the focus of most studies (e.g. Binford *et al.*, 1988; Blumenschine, 1988, 1995; Blumenschine & Selvaggio, 1991; Marean *et al.*, 1992; Capaldo, 1997; for exceptions see, Horton & Wright, 1981; Haynes, 1983; Rabinovich, 1990; Selvaggio, 1994*a*, *b*, 1998*a*). The significant damage inflicted on bones by spotted hyaenas has led to the erroneous conclusion that traces of previous feeding episodes would be obliterated if

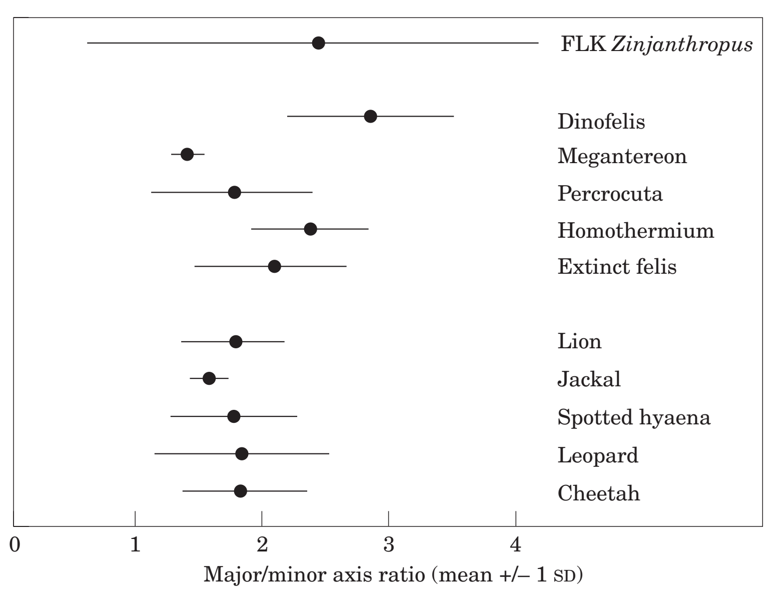

Figure 2. The ratio of the major axis to the minor axis.

hyaenas ravaged an assemblage (e.g., Binford *et al.*, 1988). This notion has become so embedded in the palaeoanthropological literature that the term "carnivore" has become somewhat synonymous with "hyaena". The research presented here and elsewhere (Selvaggio, 1994*a*, *b*, 1998*a*) demonstrates that tooth marks inflicted on bones by carnivores other than hyaenas can survive in the archaeological record.

Differences in dentition, particularly that of flesh specialists compared to bone specialists, appear to be reflected in tooth mark morphology. While there is overlap in the single morphological trait presented in this study, current research on additional morphological characteristics may identify unique features associated with specific species. The focus on carnivore tooth marks is justified because it is unlikely that hominids frequently inflicted tooth marks on bones. The development of stone tools is generally acknowledged to be a cultural innovation necessitated by the lack of shearing dentition in the hominid line.

The data presented illustrate two points. First, that bone density is related to the size (area) of tooth pits. Therefore, large tooth marks on cancellous bone should not be automatically attributed to hyaenas. Variability in tooth mark size within an archaeological sample should be considered in inferences of the number of carnivore taxa involved with an assemblage. Secondly, the data support the inference that multiple carnivore taxa were involved with the FLK *Zinjanthropus* assemblage. Tooth marks on cortical bone suggest medium-sized carnivores. Hyaenas can be ruled out as the only carnivore involved with the assemblage by the great variability in the ratio of the major axis to the minor axis of marks in the *Zinj* sample.

Considered together, the results support arguments that hominids at the *Zinj* site scavenged carcasses abandoned by leopards (Cavallo & Blumenschine, 1989), or those abandoned by extinct medium-sized carnivores (Marean, 1989) or from carcasses cached in water by hyaenas (Selvaggio, 1998*b*). After hominids had removed the remaining flesh scraps and marrow, hyaenas ravaged the site, deleting many grease-bearing epiphyseal fragments. While the results presented here support the contention that multiple carnivore taxa were involved with the *Zinj* assemblage, similar research needs to be conducted for other early archaeological assemblages to determine if this site is unique or if it is representative of hominid and carnivore activity at other early archaeological sites.

Carnivores are relatively rare in the archaeological record. The ability to identify specific carnivores from their tooth marks on bones could provide evidence for their presence at sites even when their skeletal remains are not preserved. Distinguishing which carnivores were active at sites could broaden the base of palaeoenvironmental reconstructions and be useful for testing models of hominid and carnivore competition for carcasses.

Acknowledgements

MMS thanks the Tanzanian and Kenyan governments for field clearance and the National Science Foundation, the Wrenner Gren Foundation, the L. S. B. Leakey Foundation, Sigma Xi and Rutgers University for funding. MMS is also grateful to F. Clark Howell and Lawrence Frank for support in collecting data on carnivore dentition. We thank Rutgers CAIP Center for use of the vision laboratory and Yweting Tsai and Jian Wang for graphs and laboratory assistance. We also thank the anonymous reviewers for their useful comments.

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