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NUMBER 2

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BREATHING LIFE INTO FOSSILS:

Taphonomic Studies in Honor of
C.K. (Bob) Brain



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COVER CAPTIONS AND CREDITS.

Front cover, clockwise from top left.

Top left:

Artist's reconstruction of the depositional context of Swartkrans Cave, South Africa, with a leopard consuming a hominid carcass in a tree outside the cave: bones would subsequently wash into the cave and be incorporated in the breccia deposits. © 1985 Jay H. Matternes.

Top right: The Swartkrans cave deposits in South Africa, where excavations have yielded many hominids and other animal fossils. ©1985 David L. Brill.

Bottom right: Reconstruction of a hominid being carried by a leopard. © 1985 Jay H. Matternes.

Bottom left: Photograph of a leopard mandible and the skull cap of a hominid from Swartkrans, with the leopard's canines juxtaposed with puncture marks likely produced by a leopard carrying its hominid prey. © 1985 David L. Brill.

Center: Photo of Bob Brain holding a cast of a spotted hyena skull signed by all of the taphonomy conference participants. © 2004 Kathy Schick, Stone Age Institute.

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CHAPTER 14

EQUIFINALITY IN CARNIVORE TOOTH MARKS AND THE EXTENDED CONCEPT OF ARCHAEOLOGICAL PALIMPSESTS: IMPLICATIONS FOR MODELS OF PASSIVE SCAVENGING BY EARLY HOMINIDS

MANUEL DOMÍNGUEZ-RODRIGO, CHARLES P. EGELAND
AND TRAVIS RAYNE PICKERING

ABSTRACT

The frequency and anatomical distribution of carnivore tooth marks figure prominently in models that envision Plio-Pleistocene hominids passively scavenging from felid kills. Some of these models assert that high percentages of tooth-marked limb bone midshaft fragments unambiguously reflect primary access to carcasses by carnivores (and, by extension, late access by hominids). This assertion emanates in part from analyses of tooth mark frequencies in modern “carnivore-first” carcass feeding experiments. However, because hyenas rather than felids are the predominant agent of bone modification in these actualistic controls samples, no study has yet provided the comparative tooth mark data required to accurately model hominid scavenging of abandoned felid kills. As a first step toward remedying this deficiency, we provide preliminary tooth mark data on carcasses consumed by leopards, lions and cheetahs. Our analysis demonstrates that tooth mark percentages on midshaft portions of felid-processed limb bones are (1) much lower than previously supposed and (2) even overlap in some cases with tooth mark frequencies produced by hyena ravaging of human food refuse. This potential equifinality in tooth mark frequencies and distribution highlights the palimpsest nature of many Stone Age sites and emphasizes the limited utility of tooth marks for inferring hominid foraging behavior.

INTRODUCTION

Two landmark publications in taphonomy, C.K. Brain’s (1981) *The Hunters or the Hunted?* and L.R. Binford’s (1981) *Bones*, alerted zooarchaeologists to the fact that many Stone Age faunas are palimpsests; that is, assemblages accumulated and modified by more than one formational agent. Stimulated largely by these seminal works, archaeological taphonomy has spent the last 25 years constructing referential frameworks to decipher the integrity and resolution of Stone Age archaeofaunas. In the fallout of this innovative research, the foundations of the hunting hypothesis and the concomitant socio-economic models emphasizing home bases, delayed resource consumption, and food-sharing (e.g., Isaac, 1978, 1981, 1983, 1984) were largely undermined, while new models emphasizing various forms of scavenging emerged (e.g., Binford, 1981, 1985, 1988a, b; Blumenschine, 1988, 1991, 1995; Capaldo, 1995, 1997, 1998; Potts, 1982, 1988; Potts and Shipman, 1981; Selvaggio, 1994; Selvaggio and Wilder, 2001; Shipman, 1983, 1986; Shipman and Phillips, 1976).

Much of this work was focused on documenting faunal assemblages accumulated and modified by modern humans and carnivores, with special attention paid to skeletal part abundances (e.g., Brain, 1981; Binford, 1978, 1981; Bunn, 1982, 1983; Bunn et al., 1988, 1991; Cruz-Uribe, 1991; Hill, 1975; Klein, 1975; O’Connell et al., 1988, 1990, 1992; Potts, 1982, 1988; Pickering, 2001, 2002). Further studies led to the important realiza-

tion that many bone-destroying carnivores can significantly bias skeletal part abundances in archaeofaunas by deleting less-dense axial bones and limb bone epiphyses (e.g., Bartram, 1993; Bartram and Marean, 1999; Blumenschine and Marean, 1993; Bunn, 1991, 1993; Bunn and Ezzo, 1993; Capaldo, 1995; Marean and Bertino, 1994; Marean and Frey, 1997; Marean and Spencer, 1991; Marean et al., 1992, 2004; Pickering et al., 2003; Cleghorn and Marean, this volume). However, rather than clarifying inferences of assemblage formation, this refined cognizance of carnivore bone destruction and its impact on skeletal part abundances led to disparate interpretations of early archaeological sites (e.g., Binford, 1981, 1984, 1985, 1988a,b; Blumenschine, 1991, 1995; Blumenschine and Marean, 1993; Bunn, 1981, 1982, 1983, 1986; Bunn and Kroll, 1986; Bunn and Ezzo, 1993; Isaac, 1983, 1984; Lupo, 1998; Potts, 1988; Shipman, 1986; O'Connell et al., 2002).

The research of Blumenschine and his colleagues (e.g., Blumenschine, 1988, 1995; Blumenschine and Marean, 1993; Capaldo, 1995; Selvaggio, 1994) utilized bone surface modifications to circumvent the problems of equifinality prevalent in skeletal part abundances and thus provided a powerful analytical tool for investigating the order in which carnivores and hominids intervened with carcasses. Based on actualistic assemblages of carcasses modified by humans and large carnivores in various combinations, it was argued that tooth mark frequency and anatomical distribution were the most important variables for assessing the order of hominid and carnivore access to carcasses. From these data the mode of hominid carcass acquisition was then inferred (hunting/aggressive scavenging versus passive scavenging).

This framework was elaborated by assuming "interaction" between hominids and carnivores in site formation, while criticizing previous interpretations that considered the contribution of each agent separately (Blumenschine, 1988, 1995; Blumenschine and Marean, 1993; Capaldo, 1995; Selvaggio, 1994). The application of this framework to the 1.75 million year old archaeofauna from FLK Level 22 (the *Zinjanthropus* Floor) at Olduvai Gorge, Tanzania led to a "multiple-pattern" interpretation of assemblage formation, in which defleshed and abandoned felid kills were scavenged by hominids and transported to "sites" for demarrowing with hammerstones. Hyenas intervened in the last stage of formation by consuming the grease-bearing portions of carcasses abandoned by hominids (Blumenschine, 1988, 1995; Capaldo, 1995; Selvaggio, 1994). Subsequent experiments emphasizing cutmark rather than tooth mark data led Domínguez-Rodrigo (1997a, b) to argue that hominids at FLK Level 22 were acquiring fully fleshed carcasses procured through hunting and/or aggressive scavenging. More specifically, and corroborating earlier studies (e.g., Bunn, 1981, 1982, 1986; Bunn and Kroll, 1986), Domínguez-Rodrigo (1997a, b) found that most cutmarks in the FLK Level 22 assemblage occurred on meat-bearing bone portions, indicating the presence of

substantial flesh at the time hominids imparted them.

Such contradiction among analysts, this time focusing on bone surface modifications, led researchers to highlight the effects of equifinality on analyses of cutmarks (Blumenschine, 1991, 1995; Capaldo, 1995, 1998, Selvaggio, 1994, 1998), tooth marks (Domínguez-Rodrigo, 1999a) and both cutmarks and tooth marks (Lupo and O'Connell, 2002). Nevertheless, most analysts conform to the view that high tooth mark frequencies on midshaft portions of limb bones is an indicator of primary access to carcasses by carnivores, while low tooth mark frequencies on those bone portions are indicative of secondary access by carnivores (e.g., Blumenschine, 1988, 1995; Capaldo, 1995; Lupo and O'Connell, 2002; O'Connell and Lupo, 2003).

We argue here that although previous actualistic datasets are useful interpretive tools in specific cases, there are three factors that make them inappropriate analogues for modelling passive scavenging palimpsests. First, and most importantly, the extended concept of the archaeological palimpsest recognizes that bone assemblages are both accumulated *and* modified by more than one agent (terminology follows Binford, 1980, 1981; Egeland et al., 2004). However, many of the interpretive frameworks applied to Stone Age sites, especially in Africa, assume that assemblage accumulation is largely the result of a single agent, whether carnivore or hominid. For example, it has been suggested that many Plio-Pleistocene faunas are the result of redundant predation and carcass consumption by carnivores at the same sites (e.g., Binford, 1981). Other researchers insist that hominids were the primary bone accumulators, relegating carnivores to the marginal role of modifying what was abandoned at sites (e.g., Bunn and Kroll, 1986, 1988; Potts, 1988; Oliver, 1994). Even multiple-pattern models posit a single accumulating agent (hominids) at early sites, although the initial capture and consumption of carcasses is attributed to carnivores (e.g., Blumenschine 1995; Blumenschine et al., 1994; Capaldo, 1995; Selvaggio, 1994). Therefore, such models are only partially "multi-patterned": while recognizing multiple agents of on-site bone modification, they ignore the possibility of multiple accumulation agents that may (or may not) have acted independently. Ignoring this aspect of site formation will no doubt affect interpretations based on taphonomists' standard toolkit (e.g., skeletal part abundances, minimum number of individuals, mortality profiles, carcass size profiles, bone surface modification frequencies). For example, an assemblage created through the transport of carcasses by independently operating hominids and carnivores could generate skeletal part and carcass size profiles that mimic what would be expected if hominids were scavenging from carnivore kills or dens. This problem would be exacerbated if the carnivore contribution to assemblage accumulation greatly surpassed that of the hominids. We simulate such a scenario below and its impact on the interpretation of site formation.

The second factor that limits the utility of current

actualistic models concerns the application of tooth mark frequencies and distribution. Many scavenging interpretations use tooth marks to infer the order of carnivore access, but then proceed to reconstruct the hominid role in site formation using the same data. However, hominid behavior cannot be reconstructed directly from tooth mark data (Domínguez-Rodrigo and Pickering, 2003; Pickering and Domínguez-Rodrigo, in press). Tooth mark frequencies and distributions directly reflect only carnivore interaction with bones and can thus only be used to infer carnivore access to carcasses. We demonstrate below that in a fully realized palimpsest, if the carnivore contribution to site formation exceeds that of hominids the resultant frequencies of tooth marks can mask the original hominid contribution.

Finally, the type of carnivore used in actualistic studies impacts profoundly subsequent “tests” of passive scavenging models. We present data indicating that if felids are used as the “first” carnivore in multiple-pattern models (which, according to the models themselves, should be the case) rather than hyenas, tooth mark percentages drop drastically and can become non-diagnostic. In order to provide a framework for addressing these issues, this study provides preliminary tooth mark data on carcasses consumed by leopards, lions and cheetahs.

MATERIALS AND METHODS

The analytical sample used in this study is summarized in Table 1. Briefly, a total of four separate leopard kills from South Africa and one lion kill from Kenya were analyzed. The leopard kills, consisting of three impalas and a steenbok, were discovered and reported on by Brain (1981). The lion kill, a cow, was first reported on by Domínguez-Rodrigo (1997a). In addition, prey remains from two Namibian leopard lairs and an assem-

Table 1. Summary of the felid-ravaged assemblages analyzed in this study

Predator taxon	Prey taxon	Assemblage type
Leopard	Steenbok	Kill
Leopard	Impala	Kill
Leopard	Impala	Kill
Leopard	Impala	Kill
Leopard	Goat	Den
Leopard	Sheep	Den
Cheetah	Baboon	Experimental
Lion	Cow	Kill

blage from a captive cheetah feeding experiment (Brain, 1981) are included in our sample.

Following criteria summarized by Blumenshine et al. (1996), and with the aid of 10 x hand lenses, all conspicuous and inconspicuous tooth marks on limb bone

specimens were identified. Tooth mark distributions, frequencies and densities per limb bone portion (epiphyseal, near-epiphyseal and midshaft; following Blumenshine, 1988) were also calculated (Figure 1).

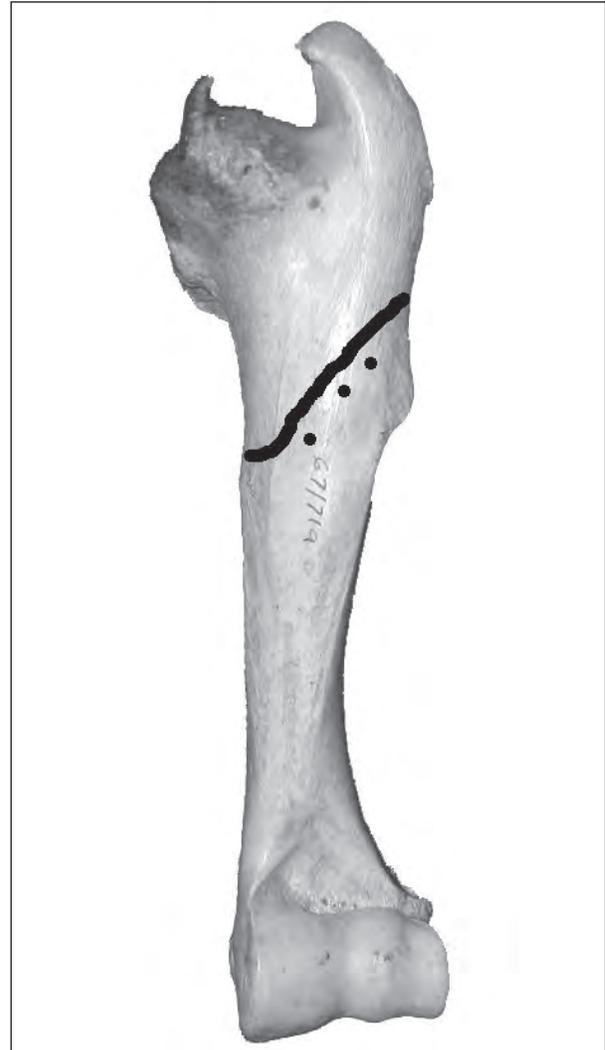


Figure 1. Cranial view of a left humerus showing how tooth marks from the felid-modified bone assemblages were located on templates. Dots indicate tooth marks and the line indicates breakage plane.

Most of the bones in the modern sample are complete (except those from the lion kill; discussed separately below). However, hammerstone breakage is an essential component of passive scavenging models. Because the complete bones in the modern sample could not actually be broken to replicate marrow extraction (after all, they comprise a valuable taphonomic study collection, created, not incidentally, by our honoree, Bob Brain), we chose to circumvent this problem by “virtually fragmenting” the comparative collection. Typical patterns of hammerstone breakage for each limb bone were established in reference to a sample of sheep carcasses that were de-

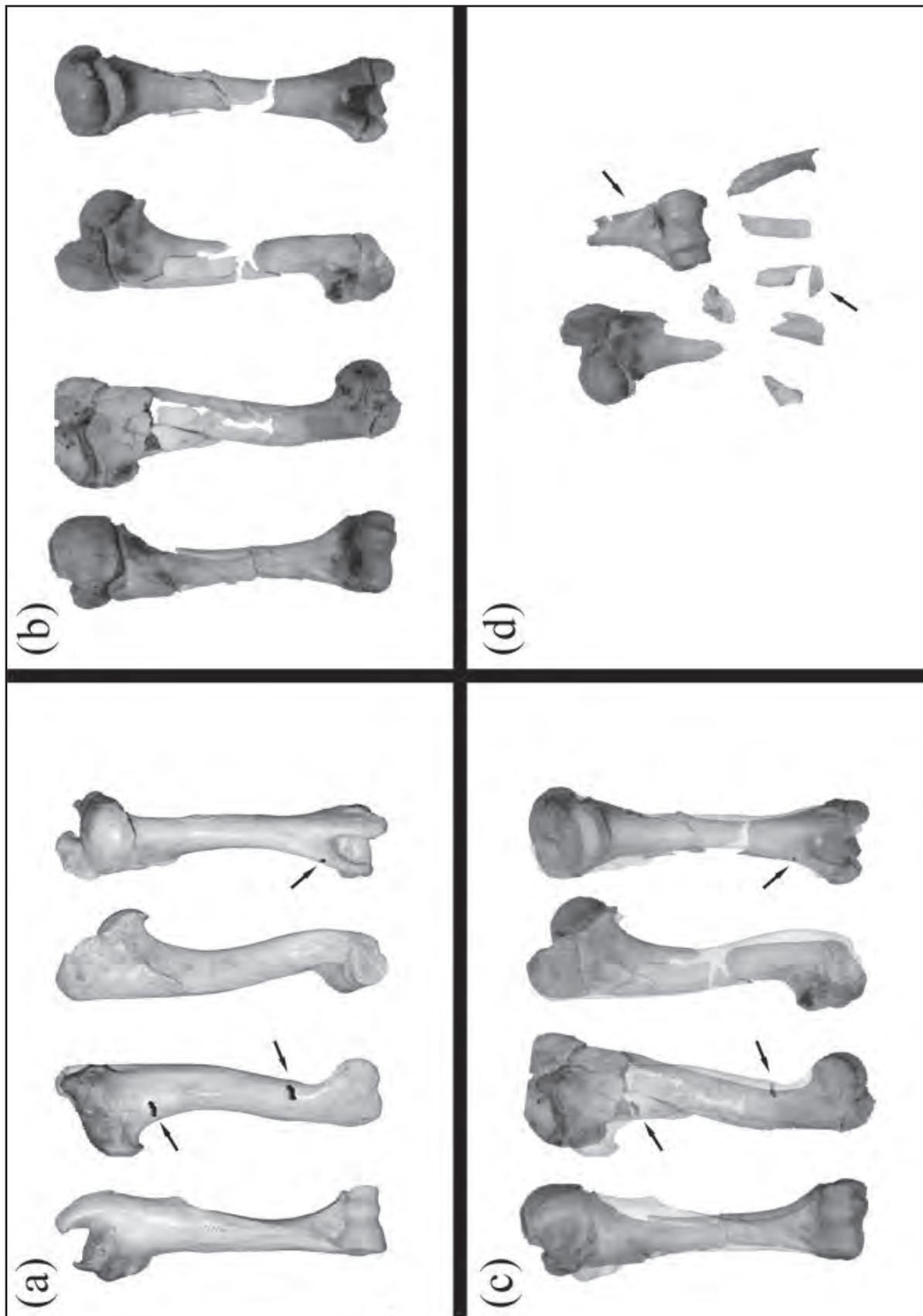


Figure 2. Summary of the “virtual fragmentation” procedure, using a left humerus as an example. (a) Exact location of each tooth mark (indicated by arrows) on a template of the complete bone showing four anatomical aspects. (b) A left humerus broken through hammerstone percussion. (c) The fragmented humerus is superimposed on the tooth-marked template (tooth marks again indicated by arrows). (d) Virtual fragmentation of the tooth-marked humerus with arrows indicating the bone fragments that are tooth-marked.

Table 2. Frequency and distribution of individual tooth marks by bone section. Abbreviations: EP = epiphysis; PNEP = proximal near-epiphysis; DNEP = distal near-epiphysis; MSH = midshaft; HM = humerus; RD = radius; MC = metacarpal; FM = femur; TA = tibia; MT = metatarsal; L = left; R = right. Note: Given the low frequency of tooth marks on epiphyses, proximal and distal ends are combined.

Assemblage	Element	Side	EP	PNEP	DNEP	MSH	Total
Steenbok	HM	L	–	–	–	1	1
	HM	R	–	–	–	–	–
	RD	L	–	–	4	–	4
Impala 1	RD	L	–	3	–	–	3
	RD	R	–	–	–	–	–
	MC	L	–	–	–	–	–
	FM	R	–	–	8	2	10
	TA	L	–	7	–	3	10
	TA	R	–	6	–	–	6
	MT	L	–	6	–	–	6
	MT	R	–	13	–	–	13
Impala 2	MC	L	–	–	–	–	–
	FM	L	–	–	–	–	–
	TA	L	–	–	–	–	–
	TA	R	–	–	–	–	–
	MT	L	–	–	–	–	–
	MT	R	–	–	–	–	–
Impala 3	MC	R	–	–	–	–	–
	TA	L	–	1	–	–	1
	TA	R	–	4	–	1	5
	MT	L	–	–	–	–	–
	MT	R	–	–	–	–	–
Goat	HM	L	2	–	6	2	10
	HM	R	–	1	1	1	3
	RD	L	–	–	–	–	–
	RD	R	–	–	–	5	5
	MC	L	–	–	–	–	–
	MC	R	–	–	–	–	–
	FM	L	–	–	5	–	5
	FM	R	–	2	5	–	7
	TA	L	–	7	1	–	8
	TA	R	–	4	1	–	5
	MT	L	–	–	–	–	–
	MT	R	–	–	–	–	–
	Sheep	HM	R	2	3	–	–
RD		R	–	–	–	–	–
MC		R	–	–	–	–	–
FM		L	–	–	6	4	10
FM		R	4	2	1	1	8
TA		L	–	1	–	2	3
TA		R	–	2	–	1	3
MT		L	–	–	–	–	–
MT		R	–	–	–	–	–
Baboon	HM	L	–	4	7	–	11
	HM	R	–	2	1	1	4
	RD	L	–	5	1	2	8
	RD	R	–	1	1	–	2
	FM	L	–	2	6	10	18
	FM	R	–	3	2	7	12
	TA	L	–	–	–	–	–
	TA	R	–	9	2	1	12
Total			8	88	58	44	198

Table 3. Tooth mark frequency and anatomical distribution in the virtually fragmented felid-ravaged assemblages. Numbers in the numerator are for the total number of tooth-marked specimens. Numbers in the denominator are for the total number of specimens in each category. Numbers in brackets show the percentage of tooth-marked specimens. Summary statistics: $n = 7$; mean %NISP tooth-marked = 15.5; standard deviation = 21.2; 95% confidence interval = 0.0 – 35.0. Abbreviations: HM = humerus; RD = radius; MC = metacarpal; FM = femur; TA = tibia; MT = metatarsal; L = left; R = right.

Assemblage	Side	HM	RD	MC	FM	TA	MT	Total
Steenbok	L	1/12 (8.3)	1/6 (16.7)	–	–	–	–	2/18 (11.1)
	R	0/10 (0.0)	–	–	–	–	–	0/10 (0.0)
	Total	1/22 (4.5)	1/6 (16.7)	–	–	–	–	2/28 (7.1)
Impala 1	L	–	0/6 (0.0)	0/7 (0.0)	–	3/8 (37.5)	2/6 (33.3)	5/27 (18.5)
	R	–	1/6 (16.7)	–	3/9 (33.3)	3/7 (42.8)	1/7 (14.2)	8/29 (27.6)
	Total	–	1/12 (8.3)	0/7 (0.0)	3/9 (33.3)	6/15 (40.0)	3/13 (23.1)	13/56 (23.2)
Impala 2	L	–	–	0/7 (0.0)	0/7 (0.0)	0/8 (0.0)	0/6 (0.0)	0/28 (0.0)
	R	–	–	–	–	0/7 (0.0)	0/7 (0.0)	0/14 (0.0)
	Total	–	–	0/7 (0.0)	0/7 (0.0)	0/15 (0.0)	0/13 (0.0)	0/42 (0.0)
Impala 3	L	–	–	–	–	1/8 (12.5)	0/6 (0.0)	1/14 (7.1)
	R	–	–	0/7 (0.0)	–	3/7 (42.8)	0/7 (0.0)	3/21 (14.3)
	Total	–	–	0/7 (0.0)	–	4/15 (26.7)	0/13 (0.0)	4/35 (11.4)
Goat	L	4/12 (33.3)	0/6 (0.0)	0/7 (0.0)	2/7 (28.5)	2/8 (20.0)	0/6 (0.0)	8/46 (17.4)
	R	2/10 (20.0)	3/6 (50.0)	0/7 (0.0)	3/9 (33.3)	2/7 (28.5)	0/7 (0.0)	10/46 (21.7)
	Total	6/22 (27.3)	3/12 (25.0)	0/14 (0.0)	5/16 (31.3)	4/15 (26.7)	0/13 (0.0)	18/92 (19.5)
Sheep	L	–	–	–	3/7 (42.9)	3/8 (37.5)	0/6 (0.0)	6/21 (28.6)
	R	1/10 (10.0)	0/6 (0.0)	0/7 (0.0)	3/9 (33.3)	2/7 (28.5)	0/7 (0.0)	6/46 (13.0)
	Total	1/10 (10.0)	0/6 (0.0)	0/7 (0.0)	6/16 (37.5)	5/15 (33.3)	0/13 (0.0)	12/67 (17.9)
Baboon	L	2/12 (16.7)	4/6 (66.7)	–	4/7 (57.1)	0/8 (0.0)	–	10/33 (30.3)
	R	2/10 (20.0)	1/6 (16.7)	–	4/9 (44.4)	3/7 (42.8)	–	10/32 (31.3)
	Total	4/22 (18.2)	5/12 (41.7)	–	8/16 (50.0)	3/15 (20.0)	–	20/65 (30.7)

Table 4. Tooth mark distribution by bone portion in the virtually fragmented felid-ravaged assemblages. Bone portion definition follows Blumenschine (1988). Numbers in the numerator are for the total number of tooth-marked specimens. Numbers in the denominator are for the total number of specimens in each category. Numbers in brackets show the percentage of tooth-marked specimens. Abbreviations: EP = epiphysis; NEP = near-epiphysis; MSH = midshaft. Summary statistics (EP): $n = 7$; mean %NISP tooth-marked = 15.9; standard deviation = 35.5; 95% confidence interval = 0.0 – 48.5. Summary statistics (NEP): $n = 7$; mean %NISP tooth-marked = 16.8; standard deviation = 19.6; 95% confidence interval = 0.0 – 34.8. Summary statistics (MSH): $n = 7$; mean %NISP tooth-marked = 8.2; standard deviation = 6.2; 95% confidence interval = 2.4 – 14.0.

Assemblage	EP	NEP	MSH	Total
Steenbok	0/6 (0.0)	1/9 (11.1)	1/13 (7.6)	2/28 (7.1)
Impala 1	3/12 (25.0)	5/10 (50.0)	5/30 (16.6)	13/56 (23.2)
Impala 2	0/12 (0.0)	0/8 (0.0)	0/22 (0.0)	0/42 (0.0)
Impala 3	1/12 (8.3)	2/7 (28.5)	1/21 (4.7)	4/35 (11.4)
Goat	9/24 (37.5)	6/21 (28.5)	3/47 (6.3)	18/92 (19.5)
Sheep	6/18 (33.3)	4/14 (28.5)	2/35 (5.7)	12/67 (17.9)
Baboon	12/16 (75.0)	0/16 (0.0)	7/42 (16.6)	20/65 (30.7)
Total	31/90 (34.4)	18/85 (21.2)	19/210 (9.0)	69/385 (17.9)

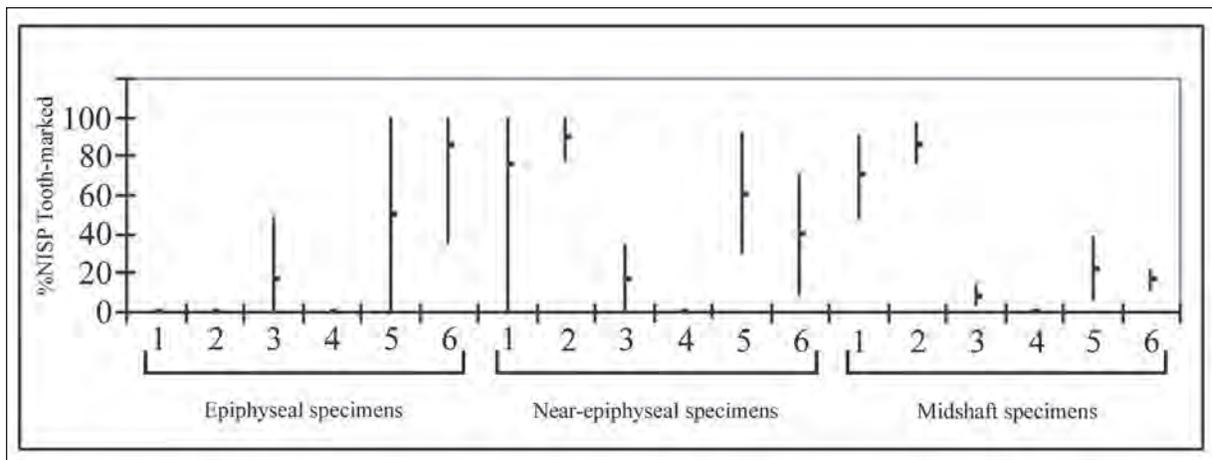


Figure 3. Means and 95% confidence intervals of tooth mark frequencies by limb bone portion for hyena- and felid-modified assemblages. Numbers: 1 = small carcasses in “carnivore-first” assemblages (Blumenschine, 1995); 2 = large carcasses in “carnivore-first assemblages” (Blumenschine, 1995); 3 = leopard and cheetah assemblages reported on here; 4 = lion assemblage reported on here; 5 = small carcasses in “hammerstone-first” assemblages (Blumenschine, 1995); 6 = large carcasses in “hammerstone-first assemblages” (Blumenschine, 1995).

fleshed and demarrowed at Complutense University as part of a butchery experiment.

These two modern datasets were combined by first drawing each individual tooth mark in the felid-ravaged sample on digital templates (displaying all four aspects) of each limb bone. Extreme care was taken to document the exact anatomical location of each tooth mark. Each limb bone was then “fractured” digitally by superimposing typical hammerstone-generated fragments onto the tooth mark templates. This procedure allows tooth mark frequencies to be reliably quantified in assemblages initially defleshed by felids and subsequently broken (virtually) by hammerstone percussion (see Figure 2).

RESULTS AND DISCUSSION

The analyzed sample of felid-ravaged limb bones from South Africa and Namibia is composed of 51 individual specimens (we discuss the lion-killed cow from Kenya below), 22 (43 %) of which preserve no tooth marks at all. This agrees with the results of Selvaggio (1994), and indicates that felids generally damage bones much less intensely than do hyenas. More specifically, a total of 198 tooth marks have been documented in the complete assemblage. Of these, only 44 (22 %) occur on midshaft sections (Table 2). A majority of the remaining tooth marks cluster on proximal and distal near-epiphyses. The relative intensity of tooth-marking on these

sections is related to the breakage of bone and, in some cases, deletion of epiphyses. However, tooth mark density is low overall. Specimens that preserve >10 tooth marks are exceptional and when this density is reached it is again related to bone chewing on the limb bone ends, often coupled with partial or total deletion of epiphyses. Complete bones, which would have been the most attractive to marrow-scavenging hominids, rarely show more than 3–5 tooth marks.

In order to model hominid scavenging of felid kills, we include in the “virtual fragmentation” only bones with intact medullary cavities, as these are the only bones that hammerstone-wielding hominids would bother to break open for marrow. Superimposing the digital templates of tooth-marked limb bones over the modern hammerstone-broken sample yields a virtual assemblage from seven felid prey carcasses that is suitable for reconstructing tooth mark frequencies and distribution in a passive

epiphyseal sections relative to midshaft sections is likely related to the fact that felid gnawing concentrates on the less dense cancellous bone of limb ends.

Our analysis of an assemblage of cow bones from a lion kill compliment the findings discussed above for smaller prey animals. We provide these data separately because unlike the South African and Namibian assemblages, the left limb bones of the lion-killed cow were actually broken open with hammerstones subsequent to lion ravaging (see details in Domínguez-Rodrigo, 1997a). As the data from Table 5 indicate, tooth mark frequencies in the lion assemblage are also very low. As with the other felid-ravaged assemblages, epiphyseal fragments display the highest tooth mark frequency followed by near-epiphyses and midshafts.

SUMMARY AND CONCLUSIONS

Implications of results for current models of passive scavenging by hominids from felid-ravaged carcasses

A previous study that investigated tooth mark densities in leopard-created bone assemblages concluded that tooth mark frequencies simi-

lar to those documented in hyena-modified assemblages would be expected on prey limb bones (Cavallo, 1997). However, this overlooks the fact that most tooth marks occur on bone fragments and not on complete bones. As we mentioned above, if hominids were scavenging from felid kills (as most passive scavenging models posit), they would disregard broken, resource-depleted bone fragments and instead concentrate on the exploitation of marrow-containing whole bones. The preliminary data presented here indicate that tooth mark frequencies in such a scenario would be very low.

This conclusion clearly calls for a reconsideration of passive scavenging models and their application to actual archaeofaunas. A fundamental aspect of multiple-pattern passive scavenging models is that felids, not hyenas, initiated the exploitation of carcasses. The empirical evidence presented here supports the theoretical assertion that hyena-modified assemblages probably do not accurately simulate felid-ravaging. Our results also have more general implications for the use of carnivore tooth mark data as indicators of hominid foraging behavior. The fact that midshaft tooth mark frequencies generated by felids acting as primary agents of bone modification are very similar to those produced by hyenas acting as secondary agents of bone modification is particularly intriguing in this regard. This seriously diminishes the utility of tooth mark frequencies on limb bone midshafts for testing scenarios of passive scavenging, especially

Table 5. Tooth mark distribution by bone portion in an assemblage modified by lions (Domínguez-Rodrigo, 1997a). Numbers in the numerator are for the total number of tooth-marked specimens. Numbers in the denominator are for the total number of specimens of each category. Numbers in brackets show the percentage of tooth-marked specimens. Abbreviations: EP = epiphysis; NEP = near-epiphysis; MSH = midshaft.

Assemblage	EP	NEP	MSH	Total
Cow	4/12 (33.3)	3/13 (23.1)	2/17 (11.7)	9/42 (21.4)

scavenging scenario. Table 3 indicates that overall tooth mark frequencies are very low in a fragmented limb bone assemblage initially consumed by felids. For all carcasses, tooth mark frequencies are <35 % (see Table 3 for summary statistics). This is in marked contrast to tooth mark frequencies in carcasses ravaged by hyenas, which show values between 80–100 % (Blumenschine, 1988, 1995).

Table 4 summarizes patterns of felid tooth mark frequency and distribution by bone portion in the virtually fragmented assemblages. Each portion (epiphyseal, near-epiphyseal and midshaft) displays lower tooth mark frequencies relative to assemblages of hyena-ravaged bones (Blumenschine, 1988, 1995). Most importantly, the mean (8.2%) and confidence intervals (2.4%–14.0%) for tooth-marked midshaft fragments are far below the >80% asserted to be a clear indication of “carnivore-first” assemblages (Blumenschine, 1988, 1995) (Figure 3). Furthermore, tooth mark frequencies in the felid-ravaged assemblages are indistinguishable from those reported for experiments that model secondary access of hyenas to hominid-demarrowed limb bones (Blumenschine, 1988, 1995). It is clear that felid defleshing of limb bones imparts few tooth marks; this finding corroborates both Selvaggio’s (1994) earlier actualistic work and unpublished observations by T.R. Pickering and K. Kuman of a captive lion assemblage from South Africa. Higher frequencies of tooth-marked epiphyseal and near-

considering that lion and hyena tooth pit dimensions on limb bone diaphyses overlap (Domínguez-Rodrigo and Piqueras, 2003). Therefore, analytical manipulations of tooth mark frequency data are subject to equifinality if the taxonomic identity of the modifying agent(s) is not recognized and controlled for explicitly in the model-building process. We thus suggest that the term “carnivore-first” is too ambiguous a concept for modelling serial intertaxonomic processing of large animal carcasses by multiple consumers.

More fundamentally, we argue that only the use of hominid-imparted bone surface modifications such as cutmarks and hammerstone percussion marks can reliably inform zooarchaeologists about the order of hominid access to large animal carcasses. This runs counter to popular zooarchaeological opinion, which contends that carnivore tooth marks are less susceptible to equifinality and thus the most useful class of surface modification for reconstructing early hominid foraging behavior (e.g., Blumenschine, 1995; Capaldo, 1995; Lupo and O’Connell, 2002).

Recent tooth mark-based interpretations of hominid behavior at FLK Level 22 can now be examined in light of the results presented here. Blumenschine (1995) asserts that tooth mark frequencies on limb bone midshaft fragments at FLK Level 22 indicate early felid and late hominid access to carcasses. Tooth mark frequencies on midshaft portions at FLK Level 22 are lower than those imparted by hyenas with primary access to bones in Blumenschine’s (1988, 1995) experiments but, as can now be seen, are also several times higher than frequencies reported here for primary felid access to carcasses. There are three reasons for this discordance in tooth mark fre-

quencies. First, as Domínguez-Rodrigo (1999b) has suggested, it is likely that hominids did not break open all limb bones at FLK Level 22, which provided scavenging hyenas with some exploitable marrow. Second, a recent reanalysis of the FLK Level 22 archaeofauna (Domínguez-Rodrigo and Barba, 2006) found that previous estimates artificially inflated tooth mark frequencies because natural biochemical marks were mistaken for tooth marks. Finally, although FLK Level 22 largely reflects the interdependent contributions of both hominids and carnivores, it is likely that as a true archaeological palimpsest in the extended sense the site also represents the independent accumulation and modification of carcasses by these agents (even if in a minority of cases), much as Isaac (1983) originally suggested for Plio-Pleistocene sites in general. Given the likely ubiquity of such a situation, we conclude by constructing a theoretical model of a true archaeological palimpsest.

Modelling an archaeological palimpsest

The important work of Blumenschine and his collaborators provides the fundamental datasets required to model an archaeological palimpsest. We restrict our simplified palimpsest to a two-agent system and begin by considering a single carcass modified by hominids and a single carcass modified by spotted hyenas. Capaldo’s (1995) extensive actualistic dataset, which includes fairly complete carcasses, is probably the best source for gauging differences in bone fragmentation by hyenas and hominids. An average of 14 limb bone fragments survive hyena ravaging per complete carcass, while human-processed carcasses yield an average of 86 limb bone fragments (Capaldo, 1995). Capaldo (1995)

Table 6. Tooth mark frequencies in a theoretical palimpsest. The initial palimpsest consists of one carcass accumulated only by hominids and one carcass accumulated only by hyenas. Each subsequent carcass represents one individual introduced to the palimpsest by hyenas, while hominids contribute no more carcasses (see text for full explanation). Total NISP represents the total number of limb bone specimens in the palimpsest. Hominid NISP represents the number of limb bone specimens introduced by hominids (this number remains the same because hominids only contribute to the initial stage of palimpsest formation). Hyena NISP represents the number of limb bone specimens introduced by hyenas (14 specimens per carcass). TM NISP represents the incremental increase in tooth-marked limb bone specimens as the number of carcasses introduced by hyenas increases. %TM represents the incremental increase in tooth mark percentages as the number of carcasses introduced by hyenas increases.

Carcass	Total NISP	Hominid NISP	Hyena NISP	TM NISP	%TM
1	100	86	14	28	28.0
2	114	86	28	39	34.2
3	128	86	42	50	39.1
4	142	86	56	61	43.0
5	156	86	70	72	46.2
6	170	86	84	83	48.8
7	184	86	98	94	51.1
8	198	86	112	105	53.0
9	212	86	126	116	54.7
10	226	86	140	127	56.2

also reports a number of identified specimens (NISP) to minimum number of elements (MNE) ratio of 1.2 limb bone fragments for each complete bone recovered after thirty experiments. Human-created assemblages result in a much higher NISP:MNE ratio (7.6). The implication of these data for a theoretical palimpsest is that human processing of a single carcass will result in more limb bone fragments than a single carcass processed by hyenas at the same accumulation site.

Regarding bone surface modifications, Capaldo (1995) reports that ~70 % of limb bone fragments recovered from hyena-modified assemblages display tooth marks, which is only slightly lower than the 84% documented in Blumenschine's (1988, 1995) experiments. In addition, both researchers demonstrate that secondary access by hyenas to human-fractured bones results in low percentages of tooth-marked limb bone fragments (~20%) and, more specifically, very low frequencies of tooth-marked midshaft fragments (10 – 15%).

When these data are combined, a theoretical assemblage of 100 limb bone specimens (86 from the carcass accumulated only by hominids plus 14 from the carcass accumulated only by hyenas) is created. Of these 100 specimens, eleven (80%) of the 14 hyena-only fragments will bear tooth marks, while 17 (20%) of the hominid-created fragments will be tooth-marked as the result of hyena scavenging. This results in a total of 28 (28% of the original 100-fragment assemblage) tooth-marked fragments.

If hyenas were to deposit the limb bones of yet another carcass (without any subsequent hominid input of carcasses), tooth mark frequencies would increase to 34.2% (39 out of 114 specimens). In other words, the addition of one carcass by hyenas would increase the previous tooth mark percentage by 6%. Table 6 summarizes the progressive increase in tooth mark frequencies with the addition of up to ten hyena-accumulated carcasses to the theoretical palimpsest. After the addition of a seventh carcass tooth mark frequencies reach 50%.

This simplified model obviously ignores a number of important factors that contribute to tooth mark frequencies. Nevertheless, the important message is that although tooth mark frequencies can be very high in palimpsests to which hyenas have contributed significantly, these frequencies do not address even indirectly the timing of hominid access to the carcasses they are responsible for accumulating. This conclusion supports our earlier contention that only hominid-imparted bone surface modifications hold the potential to construct realistic inferences of hominid carcass foraging. Our well-published arguments on the analytical utility of especially cutmark placement and frequency suggest that hominids often gained early access to carcasses (Domínguez-Rodrigo, 1997a,b, 1999a,b, 2002; Domínguez-Rodrigo and Pickering, 2003; Domínguez-Rodrigo et al., 2002, 2005; Pickering and Domínguez-Rodrigo, in press), which agree with earlier conclusions drawn by other analysts using similar data (e.g., Bunn, 1982; Bunn and Kroll, 1986).

In closing, we re-emphasize that this study represents an initial (and simplified) step towards understanding Stone Age palimpsests. However, the important point remains that when reconstructing the formation of fossil faunas, zooarchaeologists need to recognize the prehistoric reality that hominids and carnivores operated both interdependently (as currently modelled in passive scavenging scenarios), *and* independently in site formation. We also wish to stress that our critiques inherently (and gratefully) acknowledge previous actualistic work as a catalyst for this expanded view of Stone Age assemblage formation. We have in particular the pioneering work of Bob Brain to thank for the nearly universal adoption of the actualistic approach that makes this research possible.

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