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Carnivore tooth marks and stone tool butchery marks on scavenged bones: archaeological implications

This paper compares naturalistic observations on carnivore feeding behavior and carcass abandonment to results of experimental butchery of long bones collected after carcasses were abandoned by carnivores. Experiments were conducted to assess the incidence of butchery marks and carnivore tooth marks on long bones where butchery followed carnivore defleshing of limbs. One hundred and sixty-eight long bones bearing marrow and occasionally scraps of flesh were collected after carcasses were abandoned by free-ranging East African carnivores including lions, leopards, cheetahs, spotted hyenas and jackals. Flesh scraps and marrow were removed using lithic materials found commonly at Plio-Pleistocene archaeological sites. Minimally, marrow was recovered from all long bones. However, marrow was generally the only nutrient available on limbs from carcasses defleshed by nine or more carnivores. Conversely, both flesh scraps and marrow were frequently available on limbs from carcasses abandoned by solitary carnivores or groups of carnivores comprised of fewer than five animals. Data presented indicate that the incidence of butchery marks and carnivore tooth marks is related to the condition of bones upon carnivore abandonment. Quantitative data are presented on the incidence of long bone specimens bearing at least one carnivore tooth mark, one cut mark or one hammerstone percussion mark. Variability within the sample is examined with respect to the ratios of carnivore tooth marks and butchery marks on bones defleshed by different numbers of carnivores. Results indicate that variability within the sample is related to the number of carnivores involved in defleshing bones. Data presented provide a controlled basis for evaluating similar marks in archaeological bone assemblages.

Introduction

The extent to which Plio-Pleistocene hominids procured carcasses through hunting or scavenging has broad socio-ecological implications with respect to their diet, foraging strategies and social adaptations. Various criteria have been advanced for distinguishing hunting from scavenging in archaeological bone assemblages, including size/age profiles (Klein, 1982; Vrba, 1980), skeletal part profiles (Binford, 1984; Blumenschine, 1986; Potts, 1983), and marks on bone surfaces (Binford, 1981; Bunn, 1981, 1983; Shipman, 1983). While there are documented problems with each strategy (e.g., Behrensmeyer et al., 1986; Binford, 1984; Bunn & Blumenschine, 1987), carnivore tooth marks and stone-tool-butchery marks provide the most appropriate criteria, because they represent both carnivore and hominid involvement with archaeological bone assemblages and they are sensitive to the nature and timing of each agent's access to carcasses (Selvaggio n.d.a). Recognition of the archaeological traces of early access versus late access (Potts, 1983) to carcasses by Plio-Pleistocene hominids is necessary for the development of plausible models of early hominid behavioral ecology.

Recent experiments designed to identify the effects of carnivore disturbance on butchered bones have established major taphonomic indicators of carnivore bone modification and bone deletion when carnivores are exclusively the final consumers of bone nutrients (Binford et al.,

1988; Blumenschine, 1988; Blumenschine & Selvaggio, 1991; Marean & Spencer, 1991). However, experimental butchery of the bones prior to carnivore ravaging of assemblages mimics taphonomic patterns where hominids have initial access to flesh and marrow from carcasses and carnivore involvement is limited to extraction of any remaining nutrients. Therefore, cut marks on the bones reflect disarticulation and removal of major muscles, while carnivore tooth marks were inflicted during extraction of bone grease or morsels of marrow from the hammerstone-fragmented refuse. Implicitly, such experiments model early access to carcasses by hominids and secondary access to remaining nutrients by bone-crunching carnivores.

In contrast, research reported here models the reverse scenario where hominid access to carcasses follows defleshing of major muscle masses by carnivores. For experiments reported here, tooth marks represent only consumption of major muscles and disarticulation of the bones by carnivores. Likewise, cut marks represent removal of flesh scraps, skin and tendons and bone disarticulation. The most notable difference between experiments conducted by others (e.g., Blumenschine, 1988; Binford et al., 1988) and those reported here, is that carnivore involvement is restricted to final access to bones in the former and initial access to bones in the latter. As well, few carnivore species are represented in previous research where the effects of bone-crunching carnivores on butchered assemblages was the goal of such studies. Most large East African carnivores are represented in the research reported here including lions, leopards, cheetahs, jackals and spotted hyenas. A similarity shared by previous research and that reported here, is that cut marks were inflicted on whole long bones prior to marrow extraction.

Both cut marks and carnivore tooth marks have been a major focus of research on the timing and sequence of hominid and carnivore involvement with archaeological bone assemblages (e.g., Binford, 1981; Bunn et al., 1980; Bunn, 1981; Bunn & Kroll, 1986; Haynes, 1980; Potts, 1988; Potts & Shipman, 1981; Shipman, 1986). However, such studies have not resulted in a consensus on the relative contributions of hominids and carnivores to Plio-Pleistocene bone assemblages (e.g., Binford, 1981; Binford et al., 1988; Bunn & Kroll, 1986).

Percussion marks provide a new source of evidence for carcass processing that has not been previously integrated into research on hunting and scavenging by early hominids. Percussion marks are inflicted on bones during hammerstone impact and occur as patches of micro-striations or as pits or grooves containing dense patches of microstriations (Blumenschine & Selvaggio, 1988, 1991). Given good bone surface condition, percussion marks provide direct evidence for marrow extraction by hominids. Identification of percussion marks and documentation of their comparative frequency relative to carnivore tooth marks and cut marks in archaeological bone assemblages is essential for recognizing whether marrow or flesh was the primary focus of carcass processing by hominids.

Data presented are part of a broad research strategy designed to identify traces of hunting and scavenging by hominids that can be recognized in archaeological bone assemblages. This paper represents the first systematic analysis of stone-tool-butchery marks and carnivore tooth marks on long bones initially defleshed by different numbers of free-ranging carnivores. Quantitative data are presented on the incidence of long bone specimens bearing at least one carnivore tooth mark, one stone tool cut mark and one hammerstone percussion mark. Since individual bone specimens can exhibit more than one type of mark, variability within the sample is examined using the total number of each type of mark in the sample to construct ratios of cut marks to carnivore tooth marks and ratios

of percussion marks to cut marks. Mark inflation resulting from hammerstone impact is controlled by comparing the ratios of marks.

The sample is comprised of long bones where marrow was available after carnivore abandonment of carcasses. Bones were not subjected to carnivore ravaging after butchery. Consequently, carnivore tooth marks represent only defleshing and disarticulation of bones by carnivores. Cut marks represent the same processes and are, therefore, sensitive to the condition of the bone upon carnivore abandonment. Results indicate that the relative availability of flesh versus marrow on long bones defleshed and abandoned by different numbers of carnivores varies in a predictable way and leaves recognizable traces on the bones. The relative availability of such nutrients to hominid scavengers can be estimated where archaeological bone assemblages preserve carnivore tooth marks, cut marks and hammerstone percussion marks.

Methods

Research with free-ranging carnivores was conducted for 7 months during 1989–1990 in the Serengeti National Park and Ngorongoro Conservation Area, protected wildlife refuges located in northern Tanzania. These tropical savanna-woodland ecosystems support both migratory and resident populations of large mammalian herbivores and carnivores (Sinclair & Norton-Griffiths, 1979).

Observations were conducted from a four-wheel drive vehicle positioned to afford a good view of carnivore consumption of carcasses, yet minimize disturbance of carnivore activity. While carnivore hunting of prey animals was observed for only 19 of the carcasses in this sample, all long bones in the sample represent observed episodes of limb flesh consumption by carnivores. With the exception of femora, limb flesh is consumed late in the carnivore consumption sequence (Blumenschine, 1985). Therefore, it is not unusual to encounter a carnivore consuming a carcass where limb flesh is still intact. The analysis is restricted to long bones where carnivore defleshing was observed. The focus on long bones is justified due to their high representation in archaeological bone assemblages.

Nutrients were available on carcasses abandoned by carnivores in this sample. Generally, the major muscle masses of all skeletal elements were consumed by carnivores. However, head contents, bone marrow and sometimes scraps of flesh were available after carnivore abandonment of carcasses. Long bones containing marrow and occasionally scraps of flesh were collected when carnivores were approximately 0·5 km from the carcasses.

Lithics found commonly at Plio-Pleistocene archaeological sites, such as basalt and quartzite, were used to disarticulate limbs and remove remaining tissue. Approximately half of the butchery experiments were conducted under my supervision by a Tanzanian butcher who was naïve about the purpose of the experiments. Preliminary analysis indicated that variability within the sample is not related to different butchers.

Butchery of long bones included disarticulation and removal of any remaining flesh scraps, skin or tendons that would impede hammerstone fracture. A conservative butchery strategy was practiced for all experiments in that bones were not scraped either to remove periosteum or minute scraps of flesh. In order to systematize hammerstone fracture of the marrow cavity, the initial impact was inflicted near the proximal end of all long bones. Additional hammerstone impacts were inflicted along the bone's long axis until the marrow cavity was exposed. Long bones of small gazelle-sized prey usually required less than four hammerstone impacts in order to expose the marrow cavity. Prey species larger than gazelles commonly required at least five hammerstone impacts in order to expose the marrow cavity. Marrow was

Table 1   **Sample of scavenged long bones by number of carcasses represented, number of nutrient-
bearing limbs collected and number of specimens $\geqslant 2$ cm in length represented by long
bone portion and feeding group sizes of carnivore consumers**

| Carnivore group size | Number of carcasses | Number of limbs | Long bone portions | | | | Total specimens |
			CO	EPIPH	NEF	MSH	
Solitary	15	88	23	97	35	103	258
Small groups	13	72	12	121	22	130	285
Large groups	4	8	0	9	11	21	41
Total	32	168	35	227	68	254	584

Carnivore feeding groups are comprised of solitary consumers, small groups of two to four animals and large groups
of nine or 11 animals. CO=complete limbs (not hammerstone broken), EPIPH=epiphyseal fragments, NEF=near-
epiphyseal fragments, MSH=midshaft fragments.

removed from bones with a blunt wooden probe. After butchery, bones were cleaned by
boiling, air dried and wrapped in tissue for protection during shipment.

Carnivore tooth marks and butchery marks were distinguished by published criteria
(Binford, 1981; Bunn, 1981; Blumenschine & Selvaggio, 1988, 1991). Marks were identified
using a 16 power hand lens under strong, low incidence light. Each mark was counted once.
Where overlapping marks occurred each mark was counted separately. In seven cases, the
textured surface of bones from sub-adult animals hindered accurate identification of marks.
These specimens were excluded from the sample.

Sample

The sample is comprised of 168 long bones from 32 carcasses represented by 584 specimens
(Table 1). With the exception of 35 long bones from seven carcasses, all specimens result from
hammerstone impact. The 35 whole long bones allow comparison of data presented here to
complete long bones in archaeological bone assemblages. To control for bias in the recovery
of very small bone fragments that result from hammerstone impact, the sample is comprised
of bone specimens equal to or greater than 2 cm in length.

Long bones were identified with respect to skeletal element and bone portion. Long bone
portions are stratified into four categories: (1) complete or whole long bones, which were not
hammerstone broken, (2) epiphyseal fragments, defined here as any bone fragment exhibiting
an articular surface, (3) near-epiphyseal fragments, identifiable on bovids by cancellous tissue
on the medullary surface or by refitting and land marks in other species and, (4) midshafts or
diaphyseal fragments.

Preliminary analysis revealed that variability in the incidence of carnivore tooth marks is not
related to the size of prey and that variability in the incidence of cut marks and percussion
marks is not related to butchery by different individuals (Selvaggio n.d.a). The sample of long
bones is stratified by the number of carnivores involved in flesh consumption (Figure 1). This
stratification enables comparison of carnivore tooth marks and butchery marks on long bones
from carcasses abandoned by different numbers of carnivores. A distribution identified three
groups of carnivore consumers: (1) solitary animals, (2) small groups, consisting of two to four
animals and, (3) large groups, comprised of nine or 11 animals. Solitary consumers
experienced no competition while feeding and frequently abandoned carcasses with minimal
disarticulation and with skin, tendons and flesh scraps remaining on limbs. Only a moderate
degree of competition, as defined by aggression among animals, was observed for small groups
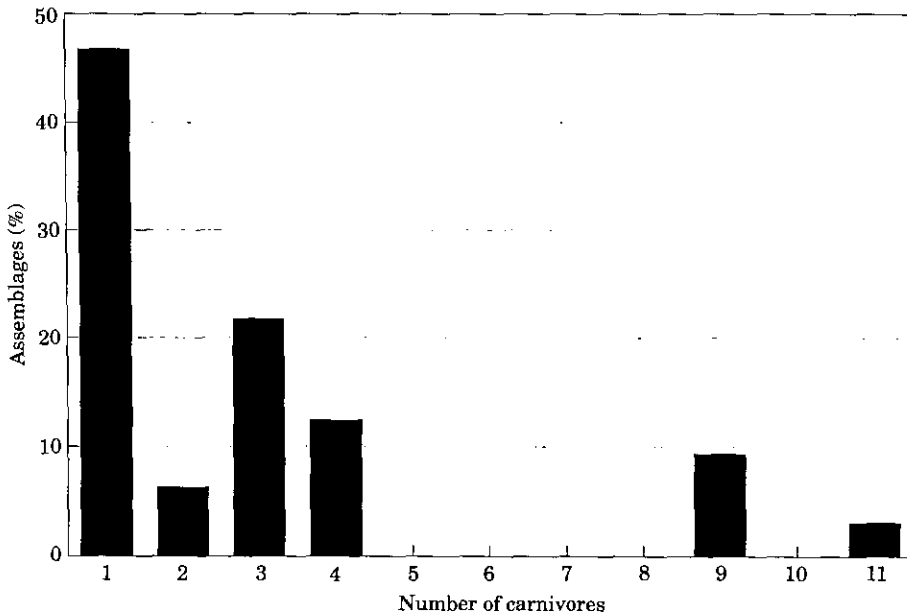
Figure 1. Distribution of the number of carnivores observed to feed on 32 carcasses.

of carnivores. Well-represented among the sample of small feeding parties are closely related animals such as females and their offspring and members of the same lion pride. Carcasses were usually abandoned by small feeding parties with minimal disarticulation and flesh scraps remaining on the bones. In this sample, large groups of consumers are comprised exclusively of members of at least two different carnivore taxa: felids, spotted hyenas and/or jackals. Competition for carcass nutrients was most intense among large groups of carnivores. Carcasses consumed by large carnivore feeding parties were usually abandoned with limb elements disarticulated from carcasses and frequently epiphyses were heavily damaged or completely gnawed away. During this study, scavenging opportunities from large groups of carnivores were infrequent as the sample size indicates (Table 1).

Analysis
Each assemblage is comprised of long bones collected from one carcass. Two analyses are presented: (1) the mean assemblage percent and the standard deviation of assemblages comprised of specimens bearing at least one carnivore tooth mark, one cut mark or one percussion mark and, (2) the ratio of carnivore tooth marks to cut marks and the ratio of percussion marks to cut marks. Variability in the former is examined by comparing the ratio of marks inflicted on bones where different numbers of carnivores were involved in defleshing carcasses. Since individual bone specimens frequently bear more than one type of mark, data on ratios are derived from the total number of carnivore tooth marks, cut marks and percussion marks on specimens in each assemblage.

Results

When all specimens are considered, carnivore tooth-marked specimens are more frequently represented than either cut-marked specimens or percussion-marked specimens (Figure 2 and
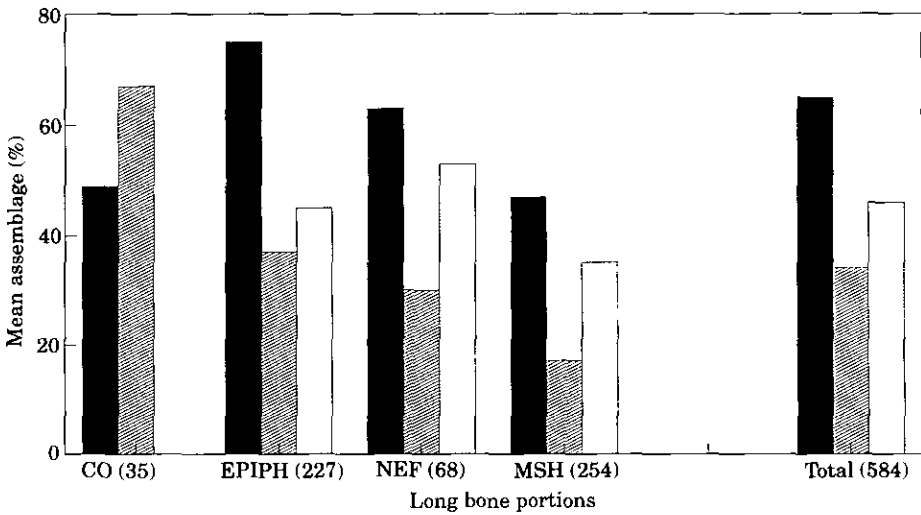
Figure 2. Mean assemblage percent of specimens bearing at least one carnivore tooth mark (■), one cut mark (▨) or one percussion mark (□). CO=complete long bones, EPIPH=epiphyses, NEF=near epiphyseal fragments, MSH=midshafts or diaphyseal fragments. See Table 2 for % ± 1 s.d.

Table 2 **The mean assemblage percent of specimens ⩾2 cm in length bearing at least one carnivore tooth mark, one cut mark or, one percussion mark, ± 1 standard deviation**

	Long bone portions				
	CO	EPIPH	NEF	MSH	Total
% Tooth-marked	49·4	75·0	63·0	47·0	65·0
± 1 S.D.	(37·0)	(25·0)	(41·0)	(27·0)	(20·0)
% Cut-marked	67·4	37·0	30·0	17·4	34·1
± 1 S.D.	(32·3)	(28·0)	(32·0)	(22·1)	(22·0)
% Percussion-marked	—	45·0	53·0	35·0	46·0
± 1 S.D.	—	(35·0)	(41·0)	(28·0)	(24·0)

Each assemblage is composed of specimens from long bones collected from one carcass ($n=32$). Complete limbs do not bear percussion marks since they were not hammerstone broken. Seven assemblages comprised of complete limbs are excluded from the percussion-marked sample.

Table 2). As well, the mean percent of specimens bearing at least one carnivore tooth mark is greater than the mean percent of specimens bearing at least one percussion mark or one cut mark for epiphyses, near epiphyses and midshafts. Among hammerstone-generated specimens, epiphyseal specimens are more frequently tooth-marked or cut-marked compared to near epiphyseal specimens or midshaft specimens. Among butchery marks, percussion-marked specimens occur more frequently than cut-marked specimens when all hammerstone-generated specimens are compared. Where long bones were not subjected to hammerstone fracture the mean percent of bones bearing cut marks is higher than the mean percent of bones bearing tooth marks.

The large standard deviations for marks on all long bone-portions indicate great variability within the sample. Variability within the sample is examined relative to the number of carnivores involved in defleshing carcasses. The ratio of cut marks to carnivore tooth marks,
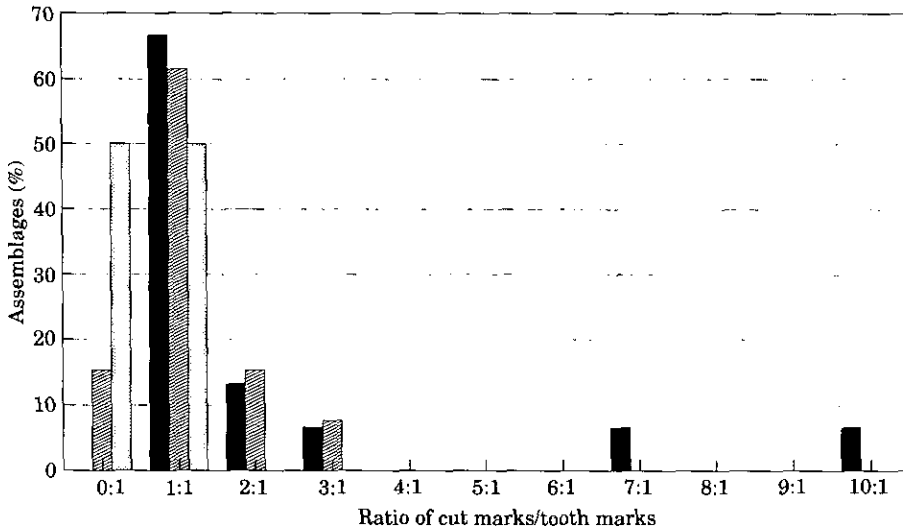
Figure 3. Ratio of cut marks to tooth marks by percent of assemblages for each carnivore group size. (■) solitary (*n*=15); (▨) small (2–4) (*n*=13); (□) large (9–11) (*n*=4).

Table 3a Ratios of cut marks to tooth marks by percent of assemblages initially defleshed by different numbers of carnivores

Carnivore group size	Ratio of cut marks/tooth marks				
	0:1	1:1	2:1	3:1	≥4:1
Solitary	—	0·68	0·13	0·07	0·12
Small group (2–4)	0·15	0·62	0·15	0·08	—
Large group (9–11)	0·50	0·50	—	—	—

Solitary animals (*n*=15), small carnivore groups (*n*=13), large carnivore groups (*n*=4).

and percussion marks to cut marks, provide an indicator with respect to the number of carnivores involved in defleshing bones, hence the relative availability of flesh on limbs after carnivore abandonment.

High ratios of cut marks to carnivore tooth marks are found on long bones where there was little or no competition among carnivores and where flesh scraps were commonly available after carnivore abandonment of carcasses (Figure 3 and Table 3a). Ratios of cut marks to carnivore tooth marks equal to or greater than 2 to 1 are found solely on bones abandoned by solitary animals and small carnivore feeding parties. The highest ratios of cut marks to carnivore tooth marks, those greater than 3 to 1, are found exclusively on long bones abandoned by solitary consumers. Conversely, long bones abandoned by large groups of carnivores exhibit the lowest ratio of cut marks to carnivore tooth marks. The number of carnivores involved in flesh consumption can be estimated in archaeological bone assemblages given the ratio of cut marks to carnivore tooth marks (Table 3b).

As well, the ratio of percussion marks to cut marks signals the condition of bones upon carnivore abandonment. A distinctively higher ratio of percussion marks to cut marks is

Table 3b   Probability of the number of carnivores involved in flesh consumption given the ratios of cut marks to carnivore tooth marks

Carnivore group size	Ratio of cut marks/tooth marks				
	0:1	1:1	2:1	3:1	≥ 4:1
Solitary	0·00	0·38	0·46	0·47	1·00
Small group (2–4)	0·23	0·34	0·54	0·53	0·00
Large group (9–11)	0·77	0·28	0·00	0·00	0·00

Probabilities are derived from data presented in Table 3a. The percent indicated in Table 3a for each carnivore group size for a specific ratio of marks is divided by the total percent of that specific ratio category.
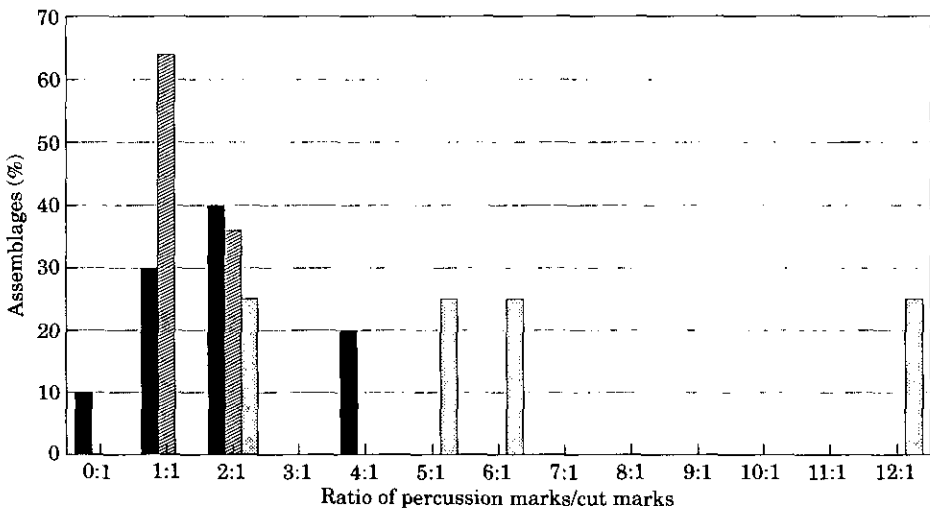

Figure 4. Ratio of percussion marks to cut marks by percent of assemblages for each carnivore group size. Seven assemblages not hammerstone-broken are excluded from this analysis. (■) solitary (n = 10); (▨) small (2–4) (n = 11); (□) large (9–11) (n = 4).

exhibited on long bones abandoned by large groups of carnivores where marrow was commonly the only remaining nutrient, in comparison to solitary animals or small groups of carnivores where both flesh scraps and marrow were usually present on bones (Figure 4 and Table 4a). Seventy-five percent of long bones from carcasses abandoned by large groups of carnivores exhibit a ratio of percussion marks to cut marks equal to or greater than 5 to 1, while all long bones abandoned by solitary animals or small groups of carnivores exhibit a ratio of less than 5 to 1. Given the ratio of percussion marks to cut marks in archaeological bone assemblages the relative availability of flesh versus marrow to a hominid scavenger can be estimated (Table 4b).

Discussion

The extent to which long bone assemblages bear butchery marks in this sample is related to the condition of the bones upon carnivore abandonment. When all specimens are considered,

Table 4a Ratios of percussion marks to cut marks by percent of assemblages initially defleshed by different numbers of carnivores

Carnivore group size	Ratio of percussion marks/cut marks					
	0:1	1:1	2:1	3:1	4:1	⩾5:1
Solitary	0·10	0·30	0·40	—	0·20	—
Small group (2–4)	—	0·64	0·36	—	—	—
Large group (9–11)	—	—	0·25	—	—	0·75

Seven assemblages not hammerstone broken are excluded from this analysis. Solitary animals ($n=10$), small carnivore groups ($n=11$), large carnivore groups ($n=4$).

Table 4b Probability of the number of carnivores involved in flesh consumption given the ratio of percussion marks to cut marks. Probabilities are derived from data presented in Table 4a

Carnivore group size	Ratio of percussion marks/cut marks					
	0:1	1:1	2:1	3:1	4:1	⩾5:1
Solitary	1·00	0·32	0·40	—	1·00	0·00
Small group (2–4)	0·00	0·68	0·36	—	0·00	0·00
Large group (9–11)	0·00	0·00	0·24	—	0·00	0·00

those bearing at least one carnivore tooth mark are more frequently represented than specimens bearing at least one percussion mark or one cut mark (Figure 2 and Table 2). Among hammerstone-generated long bone portions, the highest percentages of tooth-marked and cut-marked specimens are associated with epiphyseal portions. Epiphyses are sites of articulation and muscle attachments where tissue removal and disarticulation by both butchery and carnivore consumers is highly concentrated. Therefore, it is not unexpected that epiphyseal fragments exhibit the highest mean percentages of both cut-marked and tooth-marked specimens.

Among all hammerstone-generated long bone fragments, midshaft specimens exhibit the lowest mean percent of specimens bearing at least one cut mark or one tooth mark. The low frequency of specimens bearing at least one cut mark or one tooth mark is expected since disarticulation and muscle attachments are not associated with this portion of long bones.

Near epiphyseal fragments exhibit an intermediate percentage of cut-marked and tooth-marked specimens. Near epiphyses are sites of muscle attachments and reflect flesh removal by both carnivores and butchery. In this sample, tooth-marked near epiphyseal fragments are represented more frequently than cut-marked near epiphyseal specimens. In fact, tooth-marked specimens occur almost twice as frequently as cut-marked specimens for all hammerstone-generated long bone portions. The predominance of tooth-marked specimens for all hammerstone-generated fragments is expected since carnivores had initial access to limb flesh.

Among hammerstone-generated specimens, percussion-marked specimens are more frequently represented than cut-marked specimens. Marrow was the major nutrient available after carnivore abandonment of carcasses. Therefore, it is not unexpected that percussion-marked specimens occur as the dominant indicator of butchery in this sample.

The sample of long bones not subjected to hammerstone fracture is comprised solely of bones abandoned by solitary consumers and small groups of carnivores where disarticulation of limbs by carnivores was infrequent and flesh scraps were commonly available after carnivores abandoned carcasses (see Table 1). Disarticulation of limbs with stone flakes as well as the removal of remaining skin, tendons and flesh scraps by butchery explains the high proportion of complete bones bearing at least one cut mark.

With respect to tissue removal, both carnivore tooth marks and cut marks represent defleshing and disarticulation, while marrow extraction is solely represented by percussion marks. Taken together, the proportion of specimens bearing at least one carnivore tooth mark or one butchery mark among long bone portions reflects initial defleshing of major muscle masses by carnivores and removal of remaining tissue by butchery. However, standard deviations for marks on all long bone portions indicate great variability within the sample. Variability among the assemblages is related to the condition of the bones upon carnivore abandonment.

The ratio of cut marks to carnivore tooth marks reflects both the agent of disarticulation and the extent that flesh was available on long bones abandoned by different numbers of carnivores (Figure 3 and Tables 3a and 3b). The high ratio of cut marks to carnivore tooth marks on long bones collected from carcasses abandoned by solitary animals and small groups of carnivores, results from necessary disarticulation of the bones from carcasses by butchery, as well as the greater availability of flesh scraps on long bones compared to those abandoned by large carnivore feeding parties. Conversely, low ratios of cut marks to carnivore tooth marks on long bones abandoned by large numbers of carnivores is explained by intense competition among carnivores for flesh.

Data on the ratios of percussion marks to cut marks support the above analysis in that these ratios reflect the relative availability of marrow and flesh on long bones after carnivore abandonment (Figure 4 and Tables 4a and 4b). Among solitary consumers and small carnivore feeding parties where flesh scraps were commonly available, the ratio of percussion marks to cut marks is low (less than 5 to 1) for all long bones. In contrast, long bones collected from large carnivore feeding parties, where marrow was usually the only nutrient available, exhibit markedly higher ratios of percussion marks to cut marks than those on long bones abandoned by solitary consumers or small feeding parties. Seventy-five percent of long bones collected from carcasses defleshed by nine or more carnivores exhibit ratios of percussion marks to cut marks equal to or greater than 5 to 1.

Data on the ratios of marks in this sample indicate that variability in nutrient yields from carcasses abandoned by different numbers of carnivores is predictable and leaves recognizable traces on bones. As well, from these data it can be inferred that where the reverse scenario of hominid and carnivore access to carcasses exists, ratios of cut marks to carnivore tooth marks should be higher than those reported here and ratios of percussion marks to cut marks should be limited to the lowest ratio categories. Given good bone surface preservation, carnivore tooth marks, cut marks and percussion marks in archaeological bone assemblages can be used to estimate the relative yields of flesh or marrow extracted from long bones by carnivores or butchery.

Archaeological implications

The relationship of carnivore tooth marks and butchery marks on long bones reflects the competitive context of carcass consumption by different numbers of carnivores, hence the extent to which flesh and marrow were available after carnivores abandoned carcasses. Data

presented indicates marrow would be the primary nutrient available to hominid scavengers from carcasses defleshed and abandoned by large numbers of carnivores, while both flesh scraps and marrow would be more frequently encountered on carcasses abandoned by solitary animals or small carnivore feeding parties.

Secondary access to long bones by early hominids can be identified in archaeological assemblages where bone surfaces preserve traces of hominid butchery and carnivore gnawing. The effects of post-butchery disturbance by carnivores on patterns described here is minimal if archaeological analysis is restricted to midshaft specimens with good surface condition. Experiments on carnivore disturbance of butchered bones indicate that nutrient-depleted, hammerstone-generated midshaft fragments are ignored by carnivorous scavengers (Binford *et al.*, 1988; Blumenschine, 1988; Marean & Spencer, 1991; pers. obs.). Therefore, midshaft specimens preserve direct physical traces of carnivore and hominid involvement with carcasses prior to post-butchery ravaging by carnivores (Selvaggio, n.d.*a*).

Currently, the presence of both carnivore tooth marks and stone-tool-cut marks in archaeological bone assemblages defies interpretation as to whether hominids or carnivores acted first. Most notable, cut marks and carnivore gnaw damage on bones in the FLK *Zinjanthropus* asemblage have been used to support two different scenarios of hominid and carnivore access to carcasses (e.g., Bunn & Kroll, 1986; Binford *et al.*, 1988). In one scenario, hominids are considered to have had early access to fleshy carcasses either through hunting or usurping fresh kills from carnivores (e.g., Bunn & Kroll, 1986). In this scenario, carnivore tooth marks are thought to represent damage inflicted on bones after all flesh and marrow was removed by hominids. The opposing view is that carnivore gnaw damage on bones in the FLK *Zinjanthropus* assemblage represents initial access to carcasses by carnivores and cut marks represent disarticulation or removal of dry surface tissue (Binford, 1981; Binford *et al.*, 1988).

The assumption that carnivore involvement with bones in the FLK *Zinjanthropus* assemblage was primarily or exclusively restricted to post-butchery disturbance, precludes consideration of the potential range of carnivore involvement with the assemblage as demonstrated by the research reported here. Additionally, the notion that initial access to carcasses by carnivores would relegate hominids to scrounging morsels of nutrients, ignores variability in the competitive context of carnivore feeding behavior, as well as differences in the abilities of flesh-specialist and bone-crunching carnivores to utilize carcasses. Clearly, information on the extent that Plio-Pleistocene hominids had early access to fleshy carcasses or late access to carcasses abandoned by carnivores is relevant for developing plausible models of early hominid behavior.

The predominance of either hunting or scavenging animals by early hominids implies distinctively different foraging strategies and social adaptations. The ability of Plio-Pleistocene hominids to hunt adult wildebeest-sized prey suggests that they had developed cooperative social skills that exceed those of extant non-human primates. Additionally, the systematic hunting of such prey by early hominids would indicate that the contribution of flesh to their diet was similar to that of modern hunter-gatherers. While this human-like view of early hominid behavior is appealing, it does not explain how early hominids acquired the skills necessary for hunting such prey.

In contrast, scavenging implies a less central role for animal products in the diet of Plio-Pleistocene hominids. If early hominids acquired most or all of their animal foods by scavenging abandoned carnivore kills, it is likely that their diet, foraging strategies and social adaptations were markedly different from that of later prehistoric or extant hunter-gatherers.

Opportunities to scavenge abandoned predator kills have been documented by several recent actualistic studies (Blumenschine, 1985; Cavallo & Blumenschine, 1989; Selvaggio, n.d.*b*). These studies indicate that abandoned carcasses are predictably located in specific environments and can persist for long periods of time prior to their discovery by bone-crunching carnivores. Methods of predator avoidance useful while foraging for plant foods could have served early hominids equally well for collecting abandoned carcass parts. Resolution of conflicting scenarios of carcass procurement by early hominids is fundamental for developing plausible models of early hominid behavior.

Naturalistic observations on carnivore behavior and data from experimental simulations of different scenarios of hominid and carnivore access to carcasses provide a controlled basis for interpreting the sequence of hominid and carnivore involvement with archaeological bones. Specifically, such data allow comparisons between the incidence and anatomical patterning of marks inflicted on bones during tissue removal by known agents under known conditions and similar marks on archaeological bones (cf. Binford, 1981). Experimental simulations of different scenarios of hominid and carnivore access to carcasses have already been conducted (Blumenschine, 1988; Selvaggio n.d.*a*). Data from these experiments will be applied to the FLK *Zinjanthropus* bone assemblage and reported elsewhere (Blumenschine, n.d.; Selvaggio & Blumenschine, n.d.).

Identification of the timing and sequence of hominid and carnivore access to bones in archaeological assemblages compels consideration of damage inflicted on bones during defleshing and disarticulation by various carnivores, as well as an evaluation of the patterning and relationship of carnivore damage to both cut marks and hammerstone percussion marks. Recognition of hammerstone fracture of long bones is essential in order to determine if marrow extraction was the primary focus of hominid carcass processing.

Present indications of the complexity of hominid and carnivore involvement with bones recovered from Plio-Pleistocene sites justifies the systematic consideration of multiple lines of evidence related to hominid carcass procurement and site formation processes. Controlled experimental simulations and naturalistic observations can enhance the development of ecologically realistic models of assemblage formation.

Summary and conclusions

Data presented compare naturalistic observations on carnivore feeding behavior and carcass abandonment with results of experimental butchery of long bones where carnivores had initial access to carcasses. Naturalistic observations indicate that disarticulation of limbs from carcasses and the availability of flesh scraps on long bones after carnivore abandonment of carcasses are related to competition among carnivores for carcass nutrients. More nutrients were available on carcasses abandoned by less than five carnivores where little or no competition was observed among the animals, compared to feeding episodes where nine or more carnivores competed for carcass nutrients. The competitive context of carnivore feeding behavior, hence the availability of long bone flesh versus marrow after carnivore abandonment of carcasses, can be inferred from marks inflicted by carnivores and butchery on the bones.

Data presented indicate that the incidence and relationship of carnivore tooth marks and stone tool butchery marks vary in a predictable way and reflect the contribution of carnivores and butchery in tissue removal. Among specimens bearing at least one mark, carnivore tooth-marked specimens are most frequently represented (65%) compared to percussion-marked specimens (46%) and cut-marked specimens (34%). These data reflect initial defleshing

of bones by carnivores and the relative availability of marrow versus flesh after carnivore abandonment of carcasses. Variability within the sample is related to the condition of the bone upon carnivore abandonment. The highest ratio of cut marks to carnivore tooth marks ($\geqslant 7:1$) is found exclusively on bones abandoned by solitary animals where flesh scraps were commonly available. The highest ratio of percussion marks to cut marks ($\geqslant 5:1$) is exhibited on bones abandoned by nine or more animals where marrow was usually the only remaining nutrient. Where such data can be obtained from archaeological assemblages, the number of carnivores involved in defleshing carcasses can be estimated, hence the relative availability of flesh versus marrow to hominid scavengers can be inferred.

Naturalistic observations and experiments that model different scenarios of assemblage formation can decrease ambiguity about the timing and sequence of hominid and carnivore involvement within archaeological bone assemblages. Such studies, when applied to the archaeological record, can enhance sensitivity of the behavioral variability of agents that produced archaeological bone assemblages and thereby enrich inferences of early hominid behavior.

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