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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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1392 W. Dittemore Road · Gosport, IN 47433

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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Published by the Stone Age Institute.
ISBN-10: 0-9792-2761-5
ISBN-13: 978-0-9792-2761-5

CHAPTER 9

VERTEBRATE TAPHONOMIC PERSPECTIVES ON OLDOWAN HOMININ LAND USE IN THE PLIO-PLEISTOCENE OLDUVAI BASIN, TANZANIA

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ABSTRACT

We survey vertebrate taphonomic studies being conducted by the Olduvai Landscape Paleoanthropology Project (OLAPP) at Olduvai Gorge, Tanzania. These studies continue the tradition established by C.K. Brain of using taphonomy to reconstruct past environments and to identify the influence of carnivores on fossil bone assemblages, while extending it to establish some of the landscape ecological correlates of variability in Oldowan hominin activity traces in the Plio-Pleistocene Olduvai Basin. We use neotaphonomic findings in a variety of modern settings to interpret aspects of vertebrate fossil and stone artifact assemblages recovered from landscapes in the eastern lowermost Bed II Olduvai Basin by OLAPP since 1989, and to some of the Bed I and Lower Bed II bone assemblages recovered earlier by M.D. Leakey (1971). We address selective bone burial in lake-margin settings, crocodiles as taphonomic agents in wetland settings, small mammal assemblages as indicators of vegetation structure, tooth-marked and percussion-marked bone as indicators of the sequence of access by hominins and carnivores to carcass foods, and correlations of hyaenid ravaging of mammal long bones with patterns of stone artifact discard and loss by Oldowan hominins.

INTRODUCTION

Fewer than 40 years after C.K. Brain's (1967, 1969) pioneering observations of differential bone survivorship, vertebrate taphonomy has come to play a pivotal role in interpretations of hominin eco-behavioral evolution. Brain showed that density-dependent destruction of goat bones by dogs in Hottentot villages produced a skeletal part profile similar to that attributed by Dart (e.g., 1949) to hunting and tool-use by *Australopithecus africanus* at the South African Pliocene site of Makapansgat. This pioneering work was later extended to include a series of other modern bone-modifying species, with applications to other South African fossil-bearing cave sites (compiled in Brain, 1981). Brain was one of the first to demonstrate that non-hominin species could be important contributors of bones to assemblages that include hominin fossils and artifacts. Of perhaps greater conceptual importance, Brain also showed that vertebrate fossil assemblages contain diverse information about animal behavior and ecology that can be interpreted reliably if they are evaluated neotaphonomically, using systematic observations of relevant processes in modern settings. While studies of modern physical processes had been shown by geological scientists to provide effective interpretive models of physical processes acting in the past (e.g., Emiliani's [1955] paleo-temperature studies), Brain's work was the first to show in a systematic manner for paleoanthropology that reconstructions of paleo-behavior were amenable to a similar approach. For archaeology, Binford (e.g., 1981) would later formalize this approach to behavioral reconstructions under the label of middle range research, but it was Brain's work that laid the foundation for paleoanthropology's growing and increasingly productive reliance on behaviorally-oriented neotaphonomic research.

Brain focused on skeletal part profiles to identify the biological agents involved in the formation of bone assemblages. He expanded his early studies of differential destruction of bones by dogs to include bone modification by leopards, cheetah, brown hyenas, spotted hyenas, porcupines, various owls, and black eagles. He invoked bone density and timing of bone fusion in growing animals as the osteological properties underlying differential destruction of bone elements and portions thereof, properties which were likely to have influenced the survivability of bones of ancient animals being consumed by prehistoric carnivores. He also used bone surface modification to identify the actions of ancient animals. This work includes most famously his demonstration that the puncture~~s~~ fossilized in the cranium of an australopithecine (SK 54) from Swartkrans were likely inflicted by an animal with the canine morphology and inter-canine spacing of the fossil leopards also found at the site (Brain, 1970). Today, skeletal part profiles and bone surface modifications remain as the categories of information about vertebrate fossil assemblages that are most widely used in hominin behavioral reconstructions.

In this chapter, we expand on the methodological tradition established by Brain, by applying neotaphonomic studies to an understanding of the Plio-Pleistocene landscapes and traces of hominin land use recorded at Olduvai Gorge, Tanzania. Brain's use of vertebrate taphonomy to infer aspects of prehistoric hominin land use was limited by the sparse distribution of the South African limestone caves and the poor temporal resolution of their fossil deposits. His inferences were focused necessarily on the extent to which hominins were responsible for accumulating single site assemblages, and on whether various cave sites were hominin living sites. Behrensmeyer's (e.g., 1975; 1985; Behrensmeyer et al., 1979) studies in Kenya's Amboseli Basin, with applications to Plio-Pleistocene surface fossil assemblages at East Turkana, Kenya, showed that landscape-scale variations in the identity of various biotic and abiotic agencies of vertebrate bone assemblage formation can help to resolve paleolandscape mosaics and aspects of prehistoric community structure. Blumenschine (1989) showed that the skeletal part and portion composition of modern surface bone assemblages in the Serengeti are sensitive to competition among spotted hyenas for fresh carcass foods from larger mammals.

Here, we preview some of the ongoing vertebrate taphonomic studies being conducted by the Olduvai Landscape Paleoanthropology Project (OLAPP). These studies continue the tradition of using taphonomy to reconstruct past environments and to identify the influence of carnivores on fossil bone assemblages, while extending it to explore some of the landscape ecological correlates of variability in Oldowan hominin activity traces in the Plio-Pleistocene Olduvai Basin. Our taphonomic studies integrate neotaphonomic observations with applications to the vertebrate fossil and stone artifact assemblages recovered from landscapes in the eastern lowermost Bed II Olduvai Basin by OLAPP since 1989, and to some of the Bed I and Lower Bed II bone assemblages recovered earlier by M.D. Leakey (1971). These studies include the following:

1. Selective burial of bone in lake-margin settings, based on our ongoing studies of the Wildebeest Graveyard (Capaldo and Peters, 1995) at Lake Masek, Tanzania.
2. The establishment of crocodiles as taphonomic agents in wetland settings in Bed I and Lower Bed II, and its implications for the setting of early hominin activities.
3. Indications from small mammal assemblages of changes in the vegetation structure of a part of the Olduvai Basin in Bed I times.
4. Interpretive applications to two Bed I sites (FLK 22 (*Zinjanthropus* level) and FLK-N levels 1 and 2) of simulations of the sequence of access by hominins and carnivores to carcass foods based on bone surface modifications.
5. Use of end to shaft ratios for medium-sized and larger mammal long bones as an index of hyaenid and possibly large canid bone ravaging, and the use of this index as a proxy for predation risk that correlates with patterns of stone artifact discard and loss by Oldowan hominins across ecostructurally distinct landscapes of the paleo-Olduvai Basin.

BACKGROUND TO OLAPP

A long term goal of OLAPP is to understand the manner in which Oldowan hominins utilized the landscapes of the prehistoric Olduvai Lake Basin. The effort is designed to both reconstruct the landscape mosaics that existed in geologically exposed and unexposed parts of the paleo-Olduvai Basin, and to infer the nature of hominin activities in these landscapes. Landscape reconstruction is focused on variations in the basin's terrain, hydrology, and probable vegetation structure across space, and through time in response to short and long-term climate change as well as volcanically-induced landscape successions. Reconstructions of Oldowan hominin land use, focusing on diet, food acquisition, stone-tool technology and ranging patterns, are aimed at quantifying variability in hominin trace fossils (stone artifacts and butchered bones) across landscapes and through time, and relating these variations to contrasts in the resources and hazards that hominins are inferred to have encountered in the Olduvai Basin. Ultimately, our understanding of hominin interactions with these landscapes will be informative about the ecological circumstances surrounding the dependency of early *Homo* on flaked-stone tool use, their use of food resources from animals larger than the prey taken by non-human primates, and the evolution of the human central nervous system.

Vertebrate taphonomy is necessarily only one component of the larger multidisciplinary research program OLAPP is pursuing to achieve these goals. The project also emphasizes a variety of geological and paleobotanical approaches to landscape reconstruction. As with our vertebrate taphonomic work, these approaches integrate studies of the paleo-record with relevant observations of the natural environments of eastern and southern Africa. Although this chapter is restricted to OLAPP's vertebrate taphonomic studies, our multidisciplinary approach is an acknowledgement of the inferential complexity of landscape and land use reconstructions (cf. Gifford-Gonzalez, 1991).

We apply our neotaphonomic results to two sets of vertebrate fossil samples from Olduvai Gorge. One sample is derived from our selective re-analyses of bone assemblages recovered by Mary Leakey (1971) from excavations into Bed I and Lower Bed II. All of these assemblages are located in what Hay (1976) refers to as the Eastern Lake Margin (Figure 1a). The second sample is a subset of that recovered by OLAPP. It is restricted to the lowermost Bed II Eastern Lake Margin and distal Eastern Alluvial Fan (Figure 1). The sample consists of nearly 8000 vertebrate specimens (NISP) derived from approximately 465 m^3 of lowermost Bed II deposits excavated from 98 trenches. For the purposes of our analyses, the OLAPP trench sample is aggregated into a number of geographic locales depicted in Figure 1b.

DIFFERENTIAL BURIAL OF SKELETAL PARTS IN LAKE-MARGIN SETTINGS

Following Brain's lead, many studies have been conducted on the differential survivorship of bones subjected to a variety of destructive processes, particularly carnivore feeding. Very few studies have focused on the differential burial of bone (Behrensmeyer, 1983; Behrensmeyer and Dechant-Boaz, 1980) despite the fact that burial is prerequisite to fossilization. Burial potential of bone is apparently low in open-air and unvegetated settings, where exposure to subaerial weathering and trampling can lead to bone fragmentation and destruction beyond that inflicted by carnivores. Judging from modern shallow lake basins in East Africa, the lake-margin terrain that existed during Bed I and Lower Bed II times in the Olduvai Basin would have been exposed primarily as unvegetated mudflats or short grass and sedge pasturelands (Peters and Blumenschine, 1995, 1996). Bones in these setting would likely have been subjected to intense subaerial weathering and trampling except in well-vegetated (grass-covered) upper shore zones and in wet, low-lying areas (wet-mud lake shorelines, small channels, marshes). Observations of bones from drowned wildebeest at Lake Masek in northern Tanzania provide an opportunity to investigate the differential burial potential of skeletal parts.

Lake Masek is a small, relatively deep and narrow soda lake approximately 4 km long and 0.5 km wide. It is located in the southern Serengeti Plains adjoining Lake Ndutu, along the course of the drainage that subsequently flows eastward through Olduvai Gorge. Both lakes fluctuate in size with seasonal changes in rainfall. Compared to the very shallow and relatively broad Lake Ndutu, the flood zone along the north shore of Lake Masek is narrow, with a steeper gradient.

Both lakes are the site of episodic drownings of wildebeest that aggregate in the southeastern Serengeti Plains during the long rainy season. Mass drownings involving hundreds to thousands of individuals occur occasionally (for examples, see references in Capaldo and Peters (1995)). Drowning incidents that result in the death of only a few individuals are more common. Blumenschine (1986) reported on scavenging opportunities provided by a small drowning incident at Lake Masek in 1984. Capaldo and Peters (1996) reported on a small drowning incident, and on a bone assemblage along the north shore of the lake that resulted from a large drowning event in 1989 or 1990 (Capaldo and Peters, 1995). Njau (2000) later contrasted the surface and subsurface assemblages of wildebeest bones at both lakes. Since that time, we have continued to make at least once-yearly observations of the Capaldo and Peters study site. Referred to informally as the Wildebeest Graveyard, this study site lies along a 400 m stretch of the northern margin of Lake Masek, concentrated in a 30–40 m wide beach zone that has a slope of 4–6 degrees (Capaldo and Peters, 1995). The Wildebeest Graveyard is distinctive in containing a high density of relatively complete bones from a single species. Capaldo and Peters (1995) report a maximal minimum number of individuals (MNI) of 122 for a 100 m interval of the Graveyard area based on crania. The new observations reported briefly here are based on previously unpublished results.

Capaldo and Peters (1995) noted the dynamic burial potential of bone in the Wildebeest Graveyard. They reported a higher density of buried bone in the upper beach zone than in the lower beach zone, apparently due to the presence of clumps of grass on the upper beach. Here the grass traps bone and sediment, and resists the erosion and re-exposure of bone by the streamlets draining the grassy woodland above the beach. Bone was also buried in small channels that drain the upper beach. Overall, however, most of the burial was probably not permanent under current tectonic conditions. The area is in an erosional phase, with subsidence in the Ol'Balbal Depression at the downstream mouth of Olduvai Gorge determining the sub-regional drainage gradient. During years with low lake stands, the small channels cutting through the mid to upper beach have bone within them, some of which appears to be eroding out of previously grassy patches, and some of which appears to be undergoing burial in channel sediment. During exceptionally wet years, there is erosion of the beach at the high water line and drowning of the stoloniferous grass holding buried bone (now underwater on the mid to upper beach). Subsequent lowering of the lake level exposes the mid to upper beach to small-channel erosion once again. The grass succession and potential bone burial on the beach may begin again during this time. These local processes are still poorly understood, and we do not know what bone, if any, is buried in the deeper water of the lake.

Njau (2000) documented differential burial of skel-

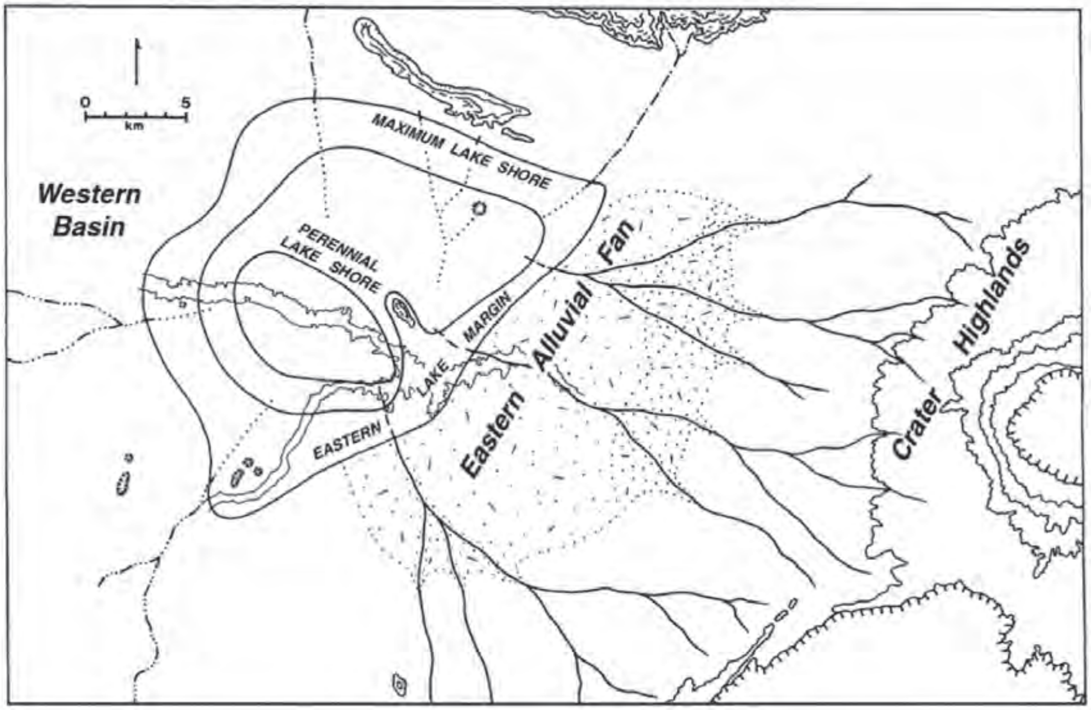
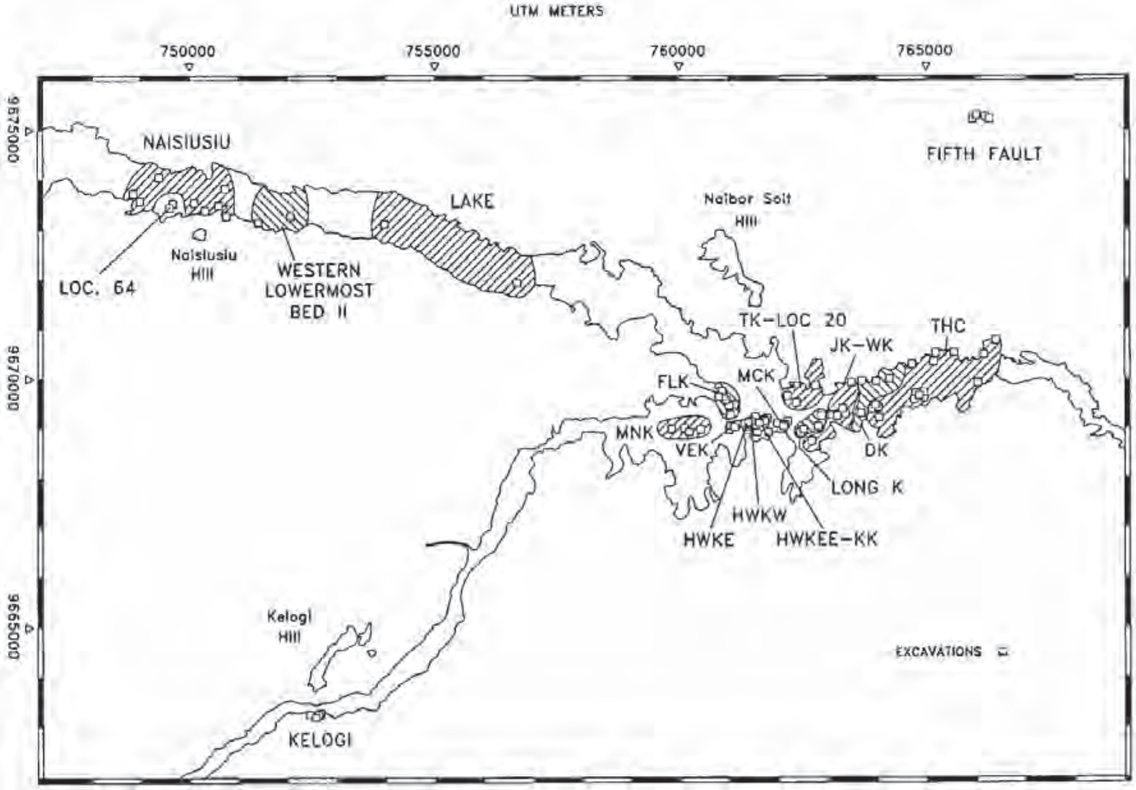


Figure 1 a. Paleogeography of the lowermost Bed II Olduvai Lake Basin (from Peters and Blumenschine, 1995, 1996; based in large part on Hay, 1976) superimposed on the outline of present-day Olduvai Gorge. The map shows the perennial (inner ring) and maximum (outer ring) paleo-lake shorelines, between which lies the lake-margin zone that was exposed during periods of relatively low lake level. The Eastern Alluvial Fan originates from streams draining the Crater Highlands on the east and southeast margins of the basin. The Western Basin extends into the Serengeti Plains. The paleogeographic zones are exposed to examination throughout the Gorge, and along fault escarpments (not shown) in the vicinity of the Gorge.



b. Olduvai Gorge, showing the location of OLAPP trenches (boxes) and the geographic locales into which they are allocated. The sample discussed in this paper derives from the Eastern Lake Margin and distal Eastern Alluvial Fan, and includes trenches in locales from MNK to THC.

etal elements in bone assemblages along the margins of Lakes Ndutu and Masek, including the Wildebeest Graveyard study site. He found buried bone in upper beach zones with small channels (Peters' observations). Relative to surface samples, vertebrae, ribs, and compact bones (tarsals, carpals, phalanges) are preferentially represented in partially and fully buried samples, while crania, scapulae, pelves, and to a lesser extent isolated teeth were underrepresented. The representation of mandibles and long bones is similar in buried and surface assemblages. The preferential burial of compact bones has been noted by Behrensmeyer (1983, Behrensmeyer and Dechant-Boaz, 1980), a phenomenon she attributes to the ease by which these bones can be pushed into a substrate by trampling. Trampling alone, however, cannot explain the preferential burial of vertebrae and ribs, given their larger size and surface area. Indeed, the preferential burial of ribs and vertebrae seems paradoxical given their relative low density and consequent lower resistance to carnivore ravaging and other subaerial destructive processes.

Figure 2 contrasts skeletal part profiles for two subsamples of the Wildebeest Graveyard. One is that provided by Capaldo and Peters (1995) for a 14 × 8 m focal plot on the upper beach. This sample represents the *in situ* remains of drowned wildebeest that had washed up on the beach during a rainy season when the lake was at a relatively high level. The second sample is provided by an unpublished inventory of bones occurring along the shoreline of the Graveyard during the long dry season in August 2001, when the lake level was lower than that when the first sample was deposited. The shoreline sample includes only those bones lying on the *c*. 1 m wide wave-wash zone of the beach, as well as those partially to fully submerged up to approximately 1 m from the shore.

The bone assemblage along the lakeshore is dominated by vertebrae and ribs. Phalanges, the unfused epiphyses of limb bone elements, and carpals/tarsals are also present, as is a single scapula and a single long bone. With the exception of the single long bone, all of these elements are easily transported by flowing water, falling into fluvial transport groups I and I/II of Voorhies (1969) and Behrensmeyer (1975).

Fluvial lag elements (transport groups II and III), including pelves, crania, and mandibles, are absent from

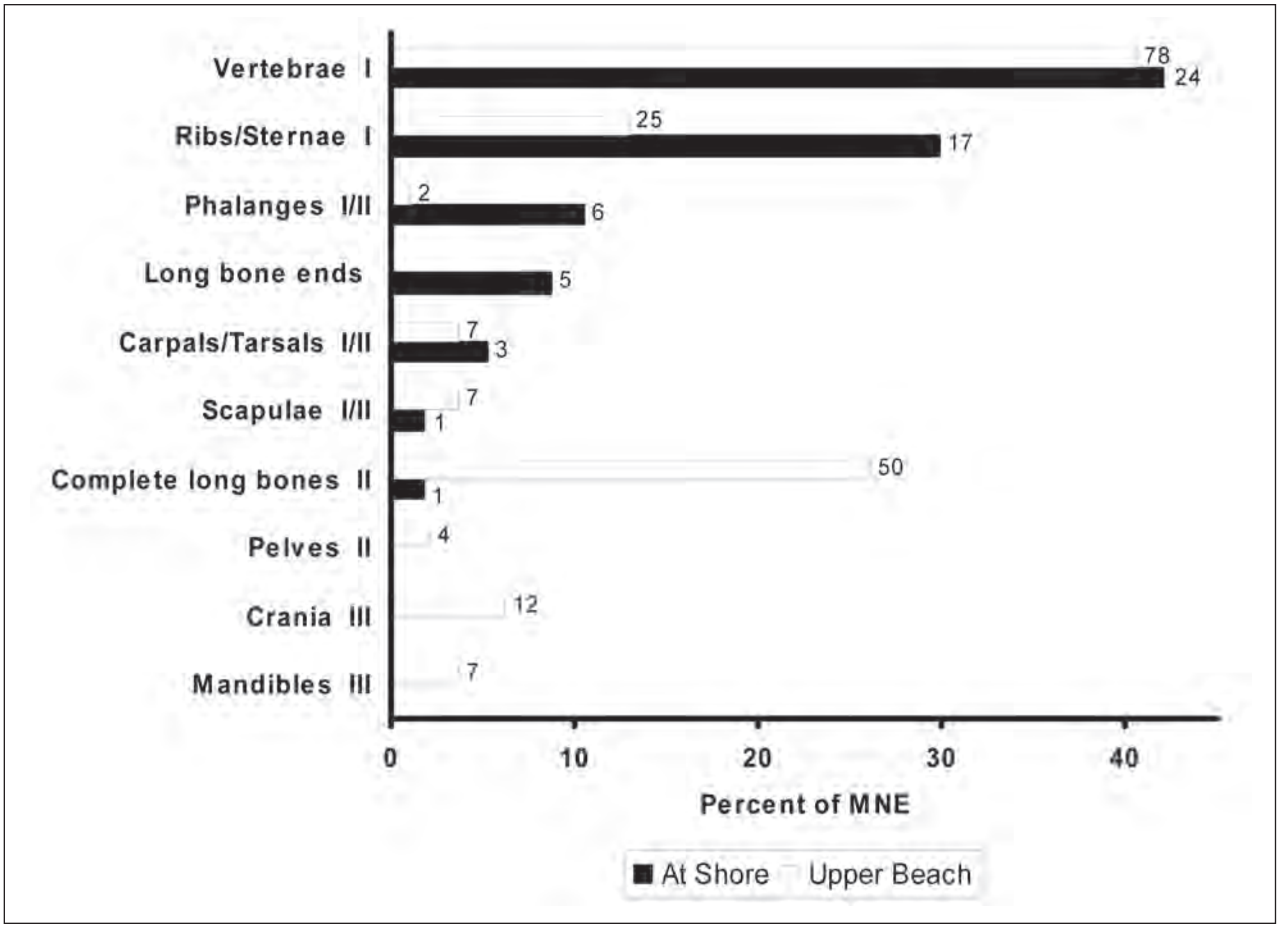


Figure 2. Skeletal unit representation (percent of total minimum number of elements, MNE) at Lake Masek's Wildebeest Graveyard, contrasting bones at the shore (18 August 2001) with those recorded from a 14 X 8 m area in the upper beach zone by Capaldo and Peters (1995: Table 4). Fluvial transport groups (I, I/II, II, II, III) of Voorhies (1969) and Behrensmeyer (1975) are indicated for each skeletal unit. Long bone ends were not recorded separately by Capaldo and Peters (1995), and have had no transport group assigned.

the shoreline sample. This pattern contrasts with the upper beach sample, which shows a more even skeletal part representation and no evidence of fluvial transport (Capaldo and Peters, 1995). Capaldo and Peters also noted that among partially buried bones, those along the lower beach are dominated by postcranial axial specimens, while those on the upper beach are dominated by long bones.

The Wildebeest Graveyard is transected by numerous streamlets that flow episodically during the rainy season. These streams apparently have a flow sufficient to entrain some bones and carry them toward the shoreline. Indeed, a number of these dry small channels contain bones transported part of the way to the shore. The shoreline assemblage contains bone that has been displaced from skeletons of animals that drowned during a rainy season when the shore was located higher on the beach. Transport mechanisms in addition to channelized flow in streamlets may also act to displace vertebrae, ribs and compact bones preferentially shoreward. These include sheetwash during heavy rainstorms, and disturbance by animals traversing the beach to drink at the lake. Regardless of the mechanism, bones that have been transported to the shore are those most likely to be pushed into mud by trampling, or buried at least partially during the next rise in lake level.

The survivorship of skeletal parts with low bone density on modern land surfaces is generally indicative of low degrees of ravaging of skeletons by bone-crunching carnivores. For example, Blumenschine (1989: Table 4) has shown that postcranial axial bones, particularly low-density ribs and vertebrae, show their highest MNE (minimum number of elements) per MNI values in Serengeti settings where carcass consumption is less complete, and bone destruction by spotted hyenas is less intense. On this basis, he proposed that relatively high proportions of postcranial axial bones in prehistoric settings may indicate that ravaging of carcasses by hyaenids was relatively low. Such prehistoric settings presumably offered greater scavenging opportunities for hominins.

For OLAPP's landscape sample from the eastern lowermost Bed II Olduvai Basin, variability in the proportion of postcranial axial to appendicular bones is evident among fossil samples from a number of geographic locales. This result might indicate that there was landscape heterogeneity in hominin scavenging opportunities. However, variation in postcranial axial skeletal part representation is strongly and positively correlated with the occurrence of bones from aquatic species (Figure 3). In light of our observations from Lake Masek, these results suggest that differential representation of skeletal elements in lowermost Bed II can be related not only to perimortem survivorship and carcass food availability to scavengers, but also to fluvial transport and burial potential of bones in lake-margin settings. Resolving this equifinality will require investigation of additional taphonomic features of the bone assemblages (e.g., degrees of fragmentation and tooth-marking), as well as detailed lithofacies analyses to identify depositional environments in which fluvial transport and differential burial of bone may have occurred.

CROCODILES AS TAPHONOMIC AGENTS IN TROPICAL WETLANDS

Numerous studies have documented bone modification by a variety of mammalian carnivores in an effort to isolate evidence for hominin feeding behavior in prehistoric bone assemblages. However, bone modification by crocodilians has not been investigated systematically. Yet, crocodilian body fossils occur in many paleoanthropological assemblages from tropical lake and river basins, and modern crocodile predation on larger mammals is common. Davidson and Solomon (1990) provide the only published description of crocodilian damage to uningested bone, but their observations are limited to a single human victim killed by a saltwater crocodile (*Crocodylus porosus*). Crocodilian damage to fossil bones is inferred rarely and only anecdotally in the paleontological literature.

Our investigation of crocodilian damage to bone was motivated by the discovery among OLAPP's fossil collections from Bed I and lowermost Bed II of several larger mammal bone specimens that bear widespread and densely-packed tooth marks, many of which are very deep and broad (Figure 4). However, these specimens are complete, lacking even the minor gnawing that is produced commonly on lower-density portions of bone by mammalian carnivores. Recognizing this paradox, Blumenschine hypothesized that the bones had been modified by crocodiles during prey capture and/or consumption. The hypothesis was based on the co-occurrence of crocodile (*Crocodylus lloidi*) body fossils in the assemblages from which these specimens derive, as well as the distinctive feeding anatomy and behavior of crocodilians. Unlike mammalian carnivores, which gnaw and break bones of larger mammal carcasses to various degrees during consumption of flesh and within-bone tissues, crocodilians attempt to swallow whole carcass units—including bones—they detach from a prey item. Carcass units too large to ingest are abandoned.

To test Blumenschine's hypothesis, Njau observed Nile crocodiles (*C. niloticus*) feeding in captive settings. Njau also inventoried fresh bone in the vicinity of pools occupied or recently abandoned by crocodiles in the lower Grumeti River, Serengeti National Park, Tanzania. The results, which are reported in detail by Njau (2006) and Njau and Blumenschine (2006), are summarized qualitatively below.

In contrast to assemblages of larger mammal bones produced by mammalian carnivores, those produced by Nile crocodiles are composed of primarily complete elements, the majority of which lack tooth marks. Those bones that are tooth-marked lack gross gnawing and bear an often high density of shallow to deep, transversely to obliquely oriented tooth scores, along with shallow

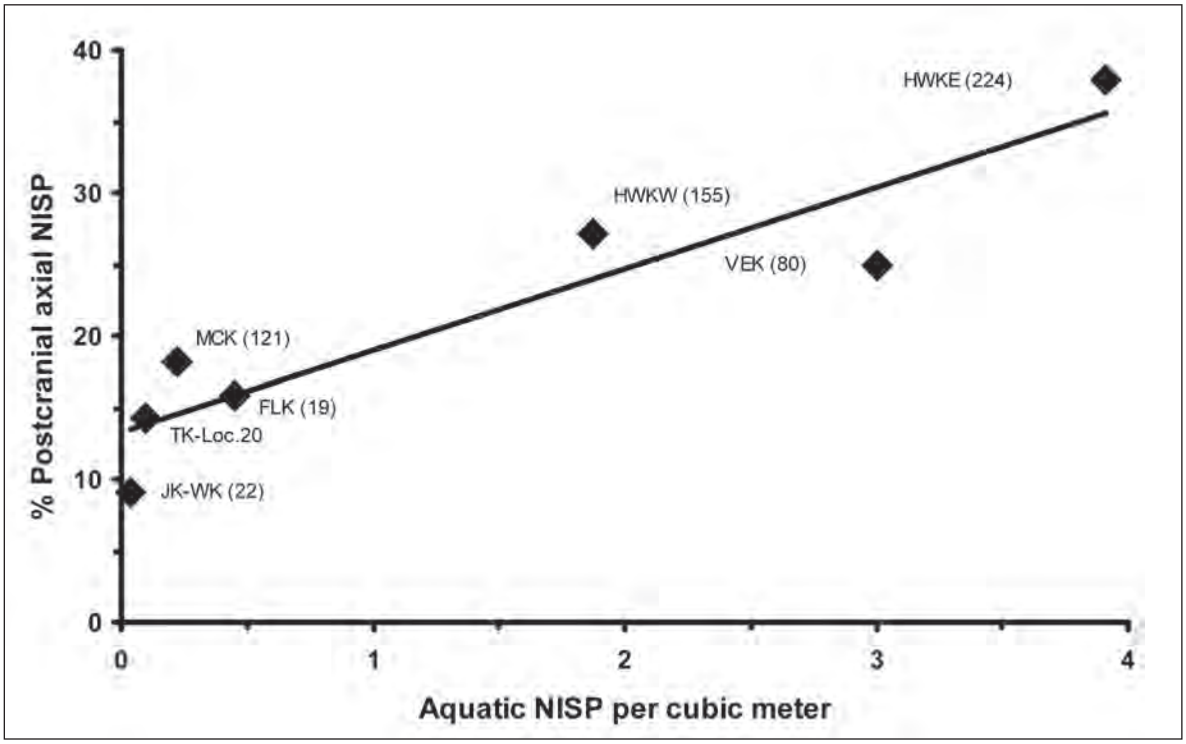


Figure 3. The relationship between the abundance of specimens (NISP values) of fossil aquatic taxa (mainly hippopotamus and crocodile, rarely fish) and the proportionate occurrence of fossil postcranial axial specimens (as % of total non-tooth NISP; numbers in parentheses) of mammals the size of extant wildebeest and buffalo from trenches spanning the whole of lowermost Bed II grouped into seven geographic locales from the eastern Olduvai Basin (Figure 1b). MNK and Long K are excluded due to sample sizes under 10 (total NISPs = 5 and 8, respectively). DK and THC Complexes are excluded due to a lack of aquatic taxa. For the regression line $y = 13.2 + 5.7x$, $r^2 = 0.86$, one-tailed $p = 0.001$.

Figure 4 a. Posterior view of a complete tibia of a fossil juvenile bovid the size of the extant eland from OLAPP Trench 21. The specimen bears post-fossilization breaks.

b. Portion of the distal shaft of the tibia showing intense tooth-marking characteristic of damage by modern Nile crocodiles. The unfused proximal epiphjysis was not recovered, but the proximal end lacks gnawing damage.

to deep pits and occasionally punctures, some of which have a morphology not observed among tooth marks produced by mammalian carnivores. The combination of intense tooth-marking and lack of gnawing and fragmentation is one of the most conspicuous traces of crocodile feeding that distinguishes it from bones fed on by mammalian carnivores. Assemblages produced by crocodiles are characterized by the retention of low-density bone portions and a number of associated bones that form articulating sets. In contrast, bone assemblages produced by mammalian carnivores are biased commonly against low-density elements and element portions, and contain fewer articulating specimens. The degree of such ravaging depends on the bone-destroying capabilities of the consumer species, and the competitiveness of the feeding episode (especially the number and hunger of consumers relative to carcass size and fat content of marrow and bone grease).

The distinctive types of feeding traces produced on fresh bones by Nile crocodiles are present on fossil specimens from Olduvai Gorge (Figure 4). We infer that these specimens were fed on by *C. lloidi*, the only crocodile known from this time period at Olduvai. We have recognized crocodile damage on a number of bone specimens recovered by OLAPP from stream and lake-margin contexts in Bed I and lowermost Bed II. Additionally, Njau (2006) reports damage consistent with that inflicted by crocodiles within all samples of larger mammal long bones he analyzed from assemblages excavated by Mary Leakey from lake-margin settings in Bed I and lower Bed II at Olduvai. These assemblages were investigated because they contain crocodile body fossils. They include DK levels 1–3, FLK 22, FLK-NN level 3, and HWK-E levels 1 and 2. In both sets of samples, damage inferred to have been inflicted by larger mammalian carnivores as well as by stone-tool-using hominins is also present, sometimes on the same bone specimen. This discovery increases the taphonomic complexity of the bone assemblages, specifically the range of bone accumulating and modifying agents that must be considered in models of site formation from localities where crocodile trace fossils are found. The great predation hazard likely posed by crocodiles to hominins (e.g., Peters and Blumenschine, 1995, 1996) also suggests that hominin activities in the vicinity of wetlands inhabited by crocodiles were more restricted than envisioned by the home base (Isaac, 1978) or living site (Leakey, 1971) models of land use. It also suggests that a significant portion of the hominin deaths represented by hominin body fossils in wetland contexts may have been the result of encounters with crocodiles.

PALEOENVIRONMENTAL IMPLICATIONS OF SMALL MAMMAL ASSEMBLAGES

To continue investigation of the environments of uppermost Bed I at Olduvai Gorge, a new but small collection of micromammals was collected by Andrews during OLAPP's 2002 field season from immediately below Tuff 1F at FLK-N. Identification of the causative agents responsible for this fauna is also considered here with reference to new data on recent owl pellet assemblages. Leakey (1971) identified six levels at FLK-N that correspond to the upper part of Bed I between Tuffs ID and IF. Levels 1 to 3, the younger of the six, were differentiated on the bases of sediment color and stone artifact density, but were also recognized as belonging to the same sedimentological level by Leakey (1971).

An earlier, more detailed study of the Bed I fossil rodent and shrew assemblages, conducted by Fernandez-Jalvo et al. (1998), documented faunal change from middle to upper Bed I. This study analyzed faunas from nine levels, six in FLK-N and three from middle Bed I in FLK-NN and FLK. The latter faunas from middle Bed I were found to contain small mammals indicative of sub-humid woodlands, with slightly drier conditions in the first part of upper Bed I in levels 4-6 in FLK-N. The top of the sequence in FLK-N levels 1-3, moreover, indicated considerably drier conditions. All three of these levels have low species richness relative to sample size, despite the fact that low rates of digestive wear on incisors suggest they were all accumulated by eagle owls (Fernandez-Jalvo et al., 1998). Eagle owls are noted for the wide range of prey species in their pellet accumulations (Andrews, 1990), both in terms of prey size and species composition. As such, the low species richness at these three levels cannot be attributed to a narrow range of predator prey-selection. Rather, it is more likely to reflect environmental conditions, with drier environments having low rodent species richness. This contrasts, for instance, with high species richness found in middle Bed I at FLK-NN level 2, where the small mammal fauna was probably accumulated by barn owls. Because barn owls are limited by their size to a lower range of prey, this indicates that the differences in species richness are a reflection of changes in the past ecosystem.

In 2002, a small excavation was made into the top of Bed I at FLK-N to confirm the stratigraphy of the Tuff IF channel cutting down into uppermost Bed I deposits (Leakey, 1971, Figure 31). The faunal sample obtained by screening is small, but it agrees in some essentials (Table 1) with the much larger ones collected by Mary Leakey from extensive excavations and described above (Fernandez-Jalvo et al., 1998). Six rodent species have been identified (Table 1), as well as one shrew and three unidentified birds. Digestion of the rodent incisors is light, with about 35% of teeth affected, and this includes a very light digestion category that has not been used previously (Andrews, 1990). This corroborates the previous conclusion that an eagle owl accumulated the small mammal fauna, most probably Verreaux eagle owl (Fernandez-Jalvo et al., 1998). On the other hand, the newly recovered sample shows how unreliable inter-taxa observations can be when derived from a small number of specimens.

Analyses of recent eagle owl and barn owl pellet assemblages are informative about the vegetation that existed in the vicinity of FLK-N during upper Bed I times. Three recent eagle owl (*Bubo lacteus*) pellet assemblages from the Serengeti were investigated earlier (Andrews, 1990), including two from kopjes in the short grass plains and one from within Olduvai Gorge. All were dominated by the gerbil *Tatera robusta*, a nocturnal species. Because of concerns that smaller owls such as barn owls could not predate this relatively large rodent, Andrews made several collections in the Serengeti in 1996 from both barn owl and eagle owl roosts. One such collection (Table 2) is from a barn owl nesting site on one of the kopjes in the short grass plains. The most abundant prey species was *Tatera robusta*, with other rodents and shrews being comparatively rare. Birds and lizards were also common, along with many remains of beetles. This collection compares well with a barn owl prey assemblage collected by Reed (2003), where gerbils were five times as abundant as murines. Finally, a collection of spotted eagle owl pellets (*Bubo africanus*) was made in 2002 within Olduvai Gorge at site MNK. It was dominated by gerbils, both large *(Tatera)* and small *(Gerbillus;* Table 3).

All of the modern prey assemblages considered above occurred in the middle of the short grass plains in the Serengeti. Those from Olduvai Gorge were accumulated by the spotted eagle owl and the Verreaux eagle owl, while those in kopjes away from the gorge were accumulated by the barn owl as well as the two eagle owls. These three predators each produced remarkably similar prey assemblages, with a super-abundance of gerbils and few if any murines. Although murines are known to be abundant in the Serengeti ecosystem (Andrews has seen large numbers of the diurnal grass mouse *Arvicanthis* in areas with high ground cover within the short grass plains), it would appear that they do not form part of the diet of any of the three owls in this part of the Serengeti. Therefore, the presence of eight other murine species in upper Bed 1 at FLK-N levels 1-3 (Table 1), as well as several non-murine and non-gerbilline species, in what is interpreted as an eagle owl prey assemblage, may indicate that the environment being sampled by the predators was not open grassland like that present today on the short grass plains. The gerbil/microtine ratio for FLK-N level 1-3 indicates a locally semi-arid environment, but it was probably one with considerable numbers of trees and/or bushes that can best be designated as wooded grassland.

SEQUENCING THE ACTIONS OF MULTIPLE CONSUMER SPECIES ON BONE ASSEMBLAGES

Again following Brain's lead, vertebrate taphonomists have made tremendous progress in describing the distinctive features of bone assemblages accumulated and modified by extant consumer species in addition to humans, including a variety of small to large mammalian carnivores, rodents and birds. These single species taphonomic descriptions have proved useful in identifying agents of bone accumulation and modification in fossil assemblages, often demonstrating that multiple consumer species were involved in an assemblage's formation. Bunn's (1981) and Potts and Shipman's (1981) identification of the presence of both stone tool cut marks and carnivore tooth marks on bones from Plio-Pleistocene assemblages is the original demonstration of this phenomenon.

Single species descriptions of assemblage formation are useful for isolating independent contributions of multiple species to a single bone accumulation. We can recognize, for example, bones deposited as owl pellets interspersed with bones of larger animals accumulated by hominins or carnivores in cave assemblages and in open-air settings that once supported roosting trees (e.g., Andrews, 1990).

Probably much more frequently than is recognized, other assemblages contain bones of animals that were fed upon by a series of consumer species, in some cases leaving feeding traces of two or more species on the same bone specimen. Such "dual-patterning" or multi-patterning (Blumenschine, 1988; Capaldo, 1997) is particularly likely to occur with assemblages containing the remains of larger mammal (> 10 kg) carcasses that once offered food surpluses to initial consumers, or within-bone nutrients they could not extract. Indeed, observations in both modern free-ranging and manipulated field settings have demonstrated the commonness by which a series of carnivore species feed on and modify the bones of the ever-diminishing remains of a single carcass. For such assemblages, single species descriptions of bone modification and accumulation are ill-suited for evaluating both the sequence of actions of multiple consumer species, and the types and amounts of carcass tissues consumed by each. This results from the fact that the parts consumed, and the associated bone modifications inflicted, by one consumer will alter both the nutritional attractiveness and the mechanical properties of bones remaining with food for a subsequent consumer (Blumenschine and Marean, 1993).

Blumenschine (1988) provided the first systematic and partially controlled field observations designed to help resolve the dual taphonomic effects of carnivores and hominins on bones of the same animal. The observations focused on the manner by which extant spotted hyenas alter the spatial distribution, long bone portion representation, and tooth and butchery mark frequencies of assemblages of long bones that had been defleshed and de-marrowed using stone tools. Using the frequencies of tooth-marked and tool-marked specimens, these observations were contrasted to simulations of a dual-patterned, "hominin-followed-by-carnivore" sequence of assemblage formation and to two single species models. The single species models include one that is "hominin only," affected only by metal-knife defleshing and hammerstone breakage of marrow cavities, and another that is "carnivore only," where lions and spotted hyenas

Table 1. *Fossil rodents recovered by M.D. Leakey (Fernandez-Jalvo et al., 1998) from FLK-N levels 1-3 combined, compared to those from OLAPP Trench 116 in levels correlative to Leakey's levels 1-3. MNI = minimum number of individuals.*

Taxon	**Leakey Assemblage MNI**	**OLAPP Assemblage MNI**
Arvicanthis primaveus	0	0
Aethomys lavocati	21	1
Mastomys minor	3	1
Mus petteri	5	0
Oenomys olduvaiensis	0	0
Pelomys dietrichi	0	0
Thallomys quadilobatus	3	0
Grammomys spp.	0	0
Zelotomys leakeyi	21	0
Total Murinae	**53**	**2**
Gerbillus spp.	39	1
Tatera gentryi	35	2
Total Gerbillinae	**74**	**3**
Steatomys spp.	37	1
Dendromus spp.	14	0
Saccostomus cf. mearnsi	22	0
Otomys petteri	63	1
Xerus cf. inauris	5	0
Heterocephalus jaegeri	2	0
Total rodents (MNI)	270	7
Total number of species	11	6
Gerbillinae/Murinae MNI ratio	1.4	1.5

Table 3. *Small mammal species composition of recent owl pellets from a crevice at MNK, Olduvai Gorge, with data on relative amounts of damage on incisors by digestion. The first ten genera listed are rodents.* Crocidura *is a shrew. MNI = minimum number of individuals.*

Taxon	**MNI**
Tatera	24
Gerbillus	25
Steatomys	15
Saccostomus	2
Aethomys	1
Dendromus	0
Arvicanthi	0
Lemniscomys	0
Mastomys	0
Mus	0
Crocidura	0

Incisor digestion	**light**	**none**	**% light**
Tatera	5	34	12.8
Gerbillus	3	21	12.5
isolated indet.	2	15	11.8

Table 2. *Minimum numbers of individuals for recent rodents (*Tatera, Gerbillus, Steatomys, Otomys*), shrews (*Crocidura*), birds and reptiles from four levels of an excavation below a barn owl nesting site at Kopje 5 in the Serengeti short grass plains.*

Level	***Tatera***	***Gerbillus***	***Steatomys***	***Otomys***	***Crocidura***	**bird**	**lizard**	**chameleon**	**Total**
level 1	13	2	0	1	1	4	2	1	24
level 2	11	6	0	0	1	4	2	0	24
level 3	49	6	3	0	2	13	6	0	79
level 4	24	4	3	0	0	1	1	0	33
Totals	97	18	6	1	4	22	11	1	160

were the sole agents of defleshing and bone breakage. At about the same time, Binford et al. (1988) reported on a smaller, more casual series of observations on carnivore disturbance of butchered bones. Subsequently, several other researchers have expanded these simulations and observations to include additional consumer sequences and additional skeletal parts, and have applied their results to several Stone Age and Paleolithic zooarchaeological assemblages (e.g. Blumenschine, 1995; Capaldo, 1997, 1998; Dominguez-Rodrigo, 1997; Marean et al., 1992, 2000; Marean and Bertino, 1994; Marean and Kim, 1998; Selvaggio, 1994, 1998).

Brain's (1967, 1969) pioneering taphonomic work with Hottentot dogs also provided a human-followed-by-carnivore scenario of assemblage formation. The bones modified by dogs had been defleshed and at least partially de-marrowed by Hottentot villagers. While the results showed that carnivore ravaging could more parsimoniously explain the disproportionate fossil skeletal part profiles at Makapansgat than selection of bones for use as tools by australopithecines, they do not by themselves rule out a role, small or large, for australopithecines in assemblage formation prior to carnivore involvement.

Here, we compare results of independent observations of carnivore tooth-marking and hammerstone percussion-marking on the FLK 22 (*Zinjanthropus* level) assemblage from Bed I, Olduvai Gorge made by Blumenschine in 1989 and Capaldo in 1997. We also provide an initial report of Capaldo's observations of hammerstone percussion-marking and carnivore tooth-marking from the FLK-N levels 1 and 2 assemblage from upper Bed I, Olduvai Gorge. Although Capaldo analyzed all larger mammal skeletal elements from both assemblages (Capaldo et al., n.d.), the results presented here are restricted to long bones, as these were the sole focus of Blumenschine's earlier study. We focus on the issue of replicability of observations on frequencies of marked bones by different analysts using our independent results from FLK 22. We also address whether the sequence of consumers indicated at FLK 22 (the most intensely studied Early Stone Age bone assemblage) is similar to that at FLK-N levels 1 and 2.

The incidences of percussion-marked and tooth-marked larger mammal long bone fragments (NISP values) from FLK 22 and FLK-N levels 1 and 2 are shown in Figures 5a and 5b, respectively. The data are presented for individual long bone portions (epiphyseal, near-epiphyseal, and midshaft fragments) following conventions used by Blumenschine (1988; see also Figure 5). The fossil samples are compared to a series of modern samples derived from simulations and natural observations in the wild conducted by Blumenschine (1988, 1995).

The data on percussion marking are compared to a "hammerstone-only" simulation sample (327 fragmentary specimens from seven trials), and a "hammerstone-followed-by-hyena" simulation sample (598 fragmentary specimens from 12 trials). Bones in these samples, derived from wild animals, were defleshed with a steel knife and broken with a hammerstone-on-stone-anvil technique to remove all marrow from the medullary cavity. Those from the latter sample were used to simulate spotted hyena ravaging of hominin food refuse, where the hyenas are attracted to the grease contained in the trabecular bone of epiphyseal fragments.

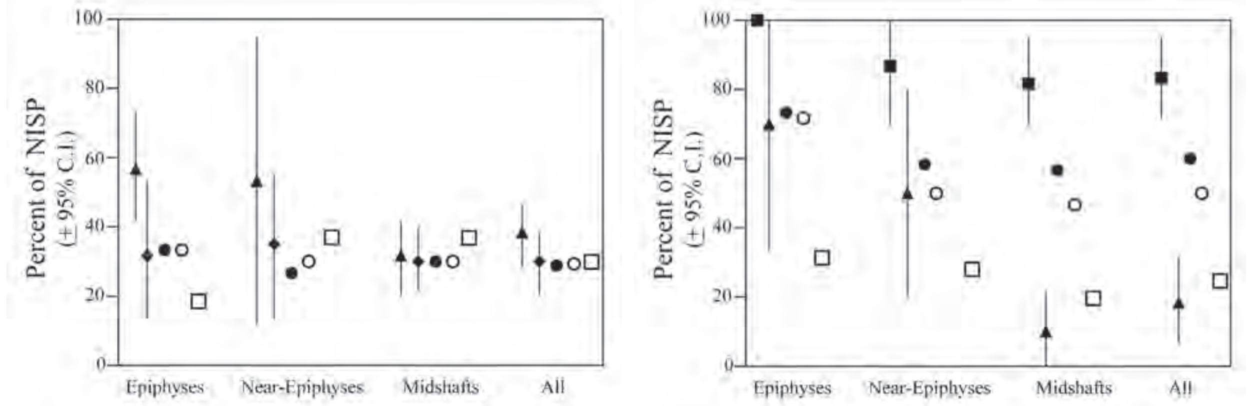
The fossil tooth mark data are also compared to two samples. These include the same "hammerstone-followed-by-hyena" sample used above, and an additional "carnivore only" sample (231 fragmentary specimens from 9 carcass consumption episodes). This sample includes bones of wild animals observed to have been defleshed and broken by lions and/or spotted hyenas to access marrow and grease.

To make the fossil samples comparable to the modern samples, we excluded from the analyses several sets of fragments. These include a) those smaller than 2 cm, b) those bearing matrix or poorly preserved surfaces that potentially hid or erased marks, and/or c) those displaying a post-fossilization break in which an estimated 10% or more of the fragment is missing; green-bone fractures characterize the specimens retained in the analytical sample. These analytical conventions are discussed more thoroughly in Blumenschine (1995) and Capaldo (1997).

Our analysis excludes a consideration of cut-marking because of the inadequacy of the modern samples of bones that have been defleshed with stone implements and subsequently broken with a hammerstone. Bones in Blumenschine's and Capaldo's samples were defleshed and disarticulated with metal knives, and as such are of questionable applicability to prehistoric defleshing that employed stone knives. Selvaggio (1994, 1998) used stone tools to remove flesh remaining on long bones fed on earlier by carnivores, but she did not provide a comparative sample for which all flesh was removed using stone tools. Domínguez-Rodrigo (1997) produced modern samples that simulate four sequences of carnivore and hominin access to long bones. His analyses are based on samples that include at least some limbs subjected to both stone-tool defleshing and hammerstone breakage for marrow extraction. Including these limbs only, two of the four simulations are represented by long bones from one carcass each, producing 73 and 42 fragmentary specimens from a total of six elements. The two other simulations are represented by long bones from two carcasses each, producing a total of 88 and 133 fragmentary specimens from a total of 14 elements. These small samples do not afford an assessment of potential variability in the incidence of cut-marked specimens introduced by differences in carcass size, thoroughness of prior defleshing by carnivores, butchery (defleshing) techniques, and degrees of fragmentation, among other factors. Further, Domínguez-Rodrigo (1997) does not describe the procedures he used to deflesh and break bones, aside from stating that stone tools were used. The small samples and lack of procedural detail needed to replicate results leaves the interpretive reliability of his neotaphonomic observations in doubt.

One striking result of the analyses in Figure 5 is the close comparability between Blumenschine's and Capaldo's independent estimates of the proportion of bones that are marked in the FLK 22 assemblage. The result is obtained despite differences in sample size: Blumenschine's analysis was based on 731 specimens, while Capaldo's 1997 analysis included 1153 specimens, adding a large number of specimens that were not stored in the Kenya National Museums along with the FLK 22 assemblage when Blumenschine conducted his earlier analysis. This comparability between our results arises because we use the same techniques for mark identification that were set out in Blumenschine et al. (1996), and we both have considerable experience in generating and studying collections of modern bones where the agent of mark production is known. The substantially lower incidence of percussion marking and tooth marking reported on the same assemblage by Oliver (1994) is probably attributable to his relative inexperience with generating and studying relevant comparative modern collections. The interanalyst correspondence between Blumenschine and Capaldo is particularly tight for percussion-marking (Figure 5a): our independent determinations for the overall incidence of percussion-marked bone differs by 1%. Our estimates for epiphyseal and midshaft fragments are essentially identical, while those for near-epiphyseal fragments differ by less than three percentage points. This correspondence reinforces the similarity between percentages of percussion-marked bones at FLK 22 and in the modern samples, a similarity that was interpreted originally by Blumenschine (1995) to indicate that hominins broke the large majority of long bones at FLK 22. The new data presented here for FLK-N levels1 and 2 similarly indicates that hominins were the main agent of long bone diaphyseal fracture (and presumably marrow consumption) at this site.

Our results on the incidence of tooth-marked long bone specimens at FLK 22 show a lower interanalyst correspondence, differing by as much as 10% (Figure 5b). Still, both analyses place the rate of tooth-marking at FLK 22 clearly intermediate to and outside of the 95% confidence intervals for the modern carnivore only and modern hammerstone-followed-by-carnivore samples. This result is consistent with the percussion mark data in indicating that carnivores were not the primary agents of bone breakage and marrow consumption at FLK 22. The significantly higher rate of tooth-marking on midshaft fragments at FLK 22 in comparison to the modern hammerstone-followed-by-carnivore sample was suggested by Blumenschine (1995) to indicate that felids had defleshed at least some of the fossilized long bones prior to their acquisition in an unbroken state by



a. Percussion Marking.

b. Tooth Marking.

Figure 5. Proportion of larger fossil mammal long bone specimens bearing at least one percussion mark (a) or tooth mark (b) at FLK 22 (Zinjanthropus level) and FLK-N, levels 1 and 2, compared with modern samples (see below). ● = FLK 22, based on Blumenschine's (1995) sample of 731 specimens. ○ = FLK 22, based on Capaldo's (1997) sample of 1153 specimens. ☐ = FLK-N, levels 1 and 2, based on a sample of 1067 specimens from Capaldo et al. (in prep.). Symbols with 95% confidence intervals represent mean values from three sets of observations of modern assemblages of fresh long bones defleshed with a steel knife and broken by hammerstone-on-stone-anvil technique, and/or by spotted hyenas (Blumenschine, 1988, 1995), as follows: ▲ = wild bovid bones defleshed with a steel knife and hammerstone-broken, followed by hyena ravaging; ◆ = wild bovid bones defleshed with a steel knife and hammerstone-broken only; ■ = wild bovid bones defleshed by lions and or spotted hyenas, and then broken by spotted hyenas only. Following the convention established by Blumenschine (1988), epiphyses are defined as any specimen bearing at least part of the proximal or distal end of the long bone; near-epiphyses are fragments derived at least in part from the proximal or distal shaft, identified on the basis of anatomical features on the cortical surface, or the presence of at least some trabecular bone on the medullary surface. Midshafts form the remainder of the fragments. Complete bones, which are few in number in both assemblages, are not included in the analysis

hominins, inflicting in the process tooth marks on the midshafts. Selvaggio's (1998) observations of long bone shafts defleshed by lions and subsequently broken with a hammerstone strongly support this interpretation. Unlike FLK 22, the similarity in percentages of midshaft tooth-marking at FLK-N levels 1 and 2 to the modern hammerstone-followed-by-carnivore sample suggests that at this fossil site, hominins had access to not only all marrow, but access also to relatively large quantities of flesh.

HYAENID BONE RAVAGING, PREDATION RISK, AND LANDSCAPE VARIATION IN ARTIFACT ASSEMBLAGES

Blumenschine and Peters (1998) used theoretical landscape variations in tree cover abundance and the inversely associated degrees of predator encounter risk for hominins to predict the landscape-specific character of stone artifact assemblages throughout the Plio-Pleistocene Olduvai Basin during lowermost Bed II times. They assumed that in settings with few trees and shrubs, carnivore density and potential competition among large carnivores for carcasses would be higher, as would hyaenid to carcass ratios. This is consistent with the reconstruction of habitat preferences for fossil hyaenids as open, relatively unwooded settings (Werdelin and Lewis, 2005).

The predictive model specified that in landscape settings with greater tree cover abundance (and therefore less predator encounter risk for hominins), the density of stone artifact discard and loss, and the functional diversity of artifact assemblages would be higher. On the other hand, detached pieces (flakes and flake fragments) were predicted to dominate assemblages in potentially more dangerous and competitive unwooded areas; here, hominins were modeled to transport still usable cores, hammerstones and manuports along with hastily acquired carcass parts to relatively safe (well wooded) areas where full butchery could take place.

Blumenschine et al. (2005) provide information on the extent to which proportions of long bone shafts to long bone ends of medium-sized (e.g., wildebeest) and large (e.g., buffalo) fossil mammals correlate with variations in Oldowan artifact density and diversity for 12 paleogeographic locales in the Olduvai Basin's lowermost Bed II Eastern Lake Margin and distal Eastern Alluvial Fan (Figure 1). The relative abundance of medium-sized and large fossil mammal long bone shafts compared to long bone ends (based on specimen counts) is used as the measure of the relative presence of hyaenids and possibly large canids in the paleo-setting. Restriction of the analysis to fossil long bones the size of those of extant wildebeest and buffalo is based on observations that show spotted hyenas to be the the only extant East African carnivore capable of fragmenting long bone diaphyses of this size (Blumenschine, 1988, 1989; Blumenschine and Marean, 1993; Marean and Spencer, 1991; Marean et al., 1992). For Plio-Pleistocene Olduvai, the relevant hyaenid was *Crocuta ultra*, a species with a similar lower third premolar (the main bone-cracking tooth) as *Crocuta crocuta*, the modern spotted hyena, and therefore similar bone-cracking capabilities (Lewis and Werdelin, 1999). *Canis africanus*, a wolf-sized canid (Werdelin, in Peters et al., 2007), was also present at Plio-Pleistocene Olduvai. This large canid may also have contributed to the fragmentation of medium-sized and large long bones judging from the bone fracturing capabilities of modern wolves (Haynes, 1980, 1983), but little published information on this fossil canid is available to evaluate this possibility. Therefore, relatively high proportions of long bone shafts to long bone ends (although difficult to translate into absolute carnivore abundance) is a reasonable index or relative measure of the increased presence of hyaenids and possibly large canids in paleo-settings. Landscape settings providing hominins with both relatively greater scavenging opportunities and a lower chance of encountering large predators theoretically would have a relatively high proportion of long bone ends.

The results of our analysis are reproduced in Figure 6. A moderately strong correlation exists between the relative abundance of long bone ends and artifact weight densities (Pearson's r = 0.69, p = 0.01). The relationship between the variables is positive, as predicted by the model, with relatively high artifact densities being associated with high proportions of long bone ends, suggesting a relative absence of hyaenids and large canids. Here, the presumed relative abundance of these carnivores apparently accounts for about half (48%) of the variability in artifact weight densities. On the other hand, the relative abundance of long bone ends shows the expected negative correlation with the proportion of whole detached pieces among all whole artifacts (Pearson's r = -0.69, p = 0.01), with the presumed relative abundance of hyaenids and possibly large canids apparently explaining about half of the variability in this measure of artifact assemblage composition. Here, hominins presumably discarded or lost a broader range of artifact functional types in locales with a relative absence of these carnivores.

Blumenschine's earlier interpretation of these results (Blumenschine et al., 2005) emphasized the role of potential competition among hominins and hyaenids for carcass resources as the major determinant of stone artifact assemblage density and functional diversity. This interpretation was based on neotaphonomic observations and conceptual frameworks developed earlier (Blumenschine, 1986, 1989, Blumenschine et al., 1994). The neotaphonomic studies suggest that the medium-sized and large mammal long bone end:shaft ratio is an indirect measure of the completeness of fresh carcass consumption by spotted hyenas, and therefore a measure of the general scale of scavenging opportunities for non-hyaenid consumers. However, emphasizing competition for carcasses assumes that traces of hominin land use were determined in large part by the availability of scavenge-

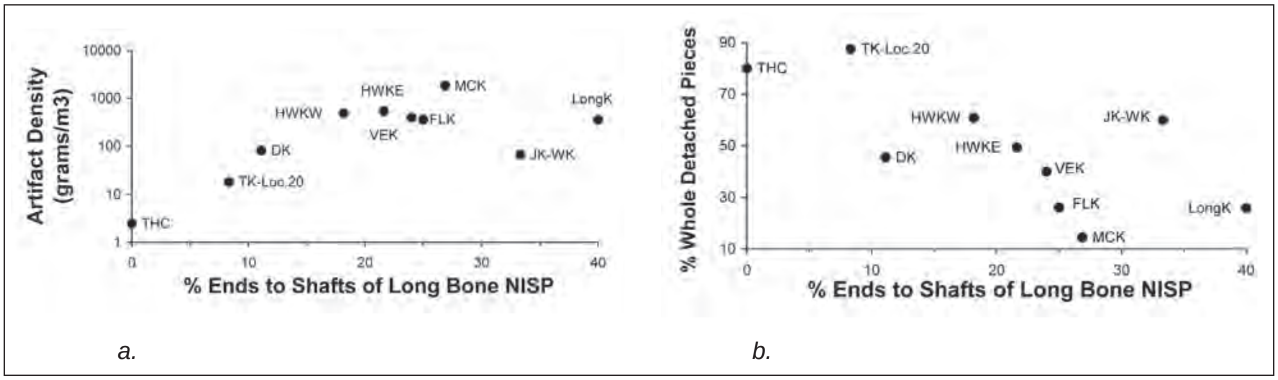


Figure 6. The relationship between the hyaenid bone-ravaging index, expressed as the percentage of articular ends among all long bone specimens, and characteristics of the artifact assemblages for 10 geographic locales in the lowermost Bed II Olduvai Basin (see Figure 1b). Artifact assemblage characteristics are (a) weight density, and (b) the percentage of whole detached pieces (flakes) among all whole artifacts. HWKEE-KK and MNK are not plotted owing to their lack of larger mammal long bone shafts.

able food. While Oldowan activity traces may largely record stone-tool butchery in landscape context (Blumenschine and Peters, 1998), constraints on utilizing other resources (water, refuge trees, plant foods, materials for tools), particularly predation risk, probably had a more regular influence on the composition and landscape distribution of stone artifact assemblages. Because of the above theoretical considerations, Werdelin and Lewis's work, and the fact that neotaphonomic studies demonstrate that hyaenid bone ravaging is greater in relatively open landscapes affording little to no arboreal refuge from predators, Peters has revised the conceptual framework to emphasize predation risk to hominins from possible encounters with large carnivores as a major determinant of Oldowan hominin land use. Now, the results of the analysis relating the relative presence of hyaenids and possibly large canids (bone-ravaging index) to the density and composition of Oldowan stone artifact assemblages are interpreted as strong evidence that differential use of the landscapes of the eastern Olduvai Basin by Oldowan hominins was conditioned in substantial part by the effects of potential predation risk. Following this interpretation, open landscape avoidance or rapid deployment and withdrawal by hominins in these settings can be related to the land use patterns of the bone-cracking hyaenids and other open-habitat large Plio-Pleistocene carnivores. One test of this interpretation will be provided by a planned analysis of carnivore tooth-marking on the fossil long bone specimens that is designed to assess the degree to which long bone fragmentation and destruction of long bone ends can be attributed to bone-cracking carnivores. If upheld, the relationships between the bone-ravaging index and stone artifact assemblage density and composition will constitute the first probable demonstration that community-level interactions involving large carnivores likely conditioned the land use patterns of prehistoric hominins.

Pobiner (2007) is currently conducting a study that may provide additional lines of evidence for evaluating the role of predator encounter risk as a possible influence on hominin land use. The study focuses on establishing taxon-specific patterns of bone damage through observations of modern carnivore feeding behavior. Taxon-specificity in bone damage is being sought at two levels: gross damage patterns to bones, and the morphology and anatomical patterning of tooth marks on bone surfaces. To date, efforts to establish taxon-specificity have been limited (Andrews and Fernandez-Jalvo, 1997; Domínguez-Rodrigo and Piquerus, 2003; Haynes, 1983; Pobiner and Blumenschine, 2003; Selvaggio and Wilder, 2001). Even family-level specificity would provide paleoecologically useful information, particularly if the relative dominance of flesh-specialist felids versus bone-cracking hyaenids in different paleo-landscape settings can be determined.

The results of Pobiner's study are not yet available, but analysis of data collected by Blumenschine in the Serengeti in 1983 and 1984 suggests that some species differences can be detected in gross damage patterns to bones. Figure 7 shows the contrasting degrees of bone damage and destruction caused by four extant carnivore species on fresh Size Class 1 (e.g., Thomson's gazelle) and Size Class 3 (e.g., wildebeest) carcasses. Figure 7 includes data on upper hindquarter parts (Pobiner and Blumenschine, 2003), plus previously unpublished data on upper forelimb parts. This figure shows a pattern within each carcass size group of progressively greater bone destruction that corresponds to increasing body size and/or jaw strength of the carnivores under consideration. Carnivores with greater bone destruction ability reduce and eventually destroy skeletal elements and skeletal element portions more intensely than do less capable bone-breakers. Destruction and marginal gnawing by lions on Size Class 3 carcasses is restricted to the same skeletal parts reduced by cheetah on Size Class 1 carcasses, with the addition of the caudal part of the sacrum and the olecranon process of the ulna. Destruction of Size Class 3 carcass parts by spotted hyenas is more intense, and includes virtually all parts destroyed or heavily fragmented by lions on Size Class 1 carcasses, with the major exception of the lumbar vertebral centra. In short, these observations demonstrate that lions damage the same bones to the same extent on Size Class 3 carcasses that cheetah damage on Size Class 1 carcasses, while spotted hyena damage and destruction of Size Class 3 carcasses mirrors the location and intensity of damage inflicted by lions on Size Class 1 carcasses. This patterning suggests the existence of a simple mechanism underlying the degree of skeletal reduction inflicted by modern carnivores when extracting flesh and within-bone edible tissues: the increased bone size and strength characteristic of larger mammalian carcasses imposes greater mechanical constraints to nutrient extraction that can be overcome only by carnivores with greater jaw strength and dental capabilities for breaking bone.

CONCLUSIONS

OLAPP's vertebrate taphonomic work will continue to focus on ways in which paleolandscape ecology and hominin land use are revealed by analyses of fossil bone assemblages. Our work focuses on the development of reliable methods for identifying the feeding traces of individual carnivore taxa, and on resolving sequences of carnivore and hominin access to carcasses, including the types and amount of tissues consumed by each. It also focuses on measuring landscape variability in the differential traces of carnivore and hominin presence and their respective patterns of land use. Brain's contributions to vertebrate taphonomy encouraged the development of models of land use for individual larger carnivore taxa, inspiring our ongoing model-building for Oldowan hominins. Future work will also lead to new understandings of evolutionary changes in the larger carnivore guild, wherein hominins played an increasingly important role. We can also expect an increasingly refined role for taphonomy in the pursuit of paleoenvironmental reconstruction.

ACKNOWLEDGEMENTS

We are grateful to a number of Tanzanian institutions for permitting and cooperating with our research. These include the Tanzania Commission for Science and Technology, the Antiquities Department, the National Museums of Tanzania, the Tanzania Wildlife Research Institute, the Ngorongoro Conservation Area Authority, Tanzania National Parks, and the Serengeti National Park. Funding for the research was provided by the National Science Foundation, the Wenner-Gren Foundation for Anthropological Research, the L.S.B. Leakey Foundation, and Rutgers University's Center for Human Evolutionary Studies. CRP also thanks the Department of Anthropology at the University of Georgia for continued support as Professor Emeritus. An anonymous reviewer provided useful comments on the manuscript. We are grateful to members of the OLAPP team who have contributed to the work reported here on modern and fossil bone assemblages at Olduvai. Finally, we thank the editors of this volume for organizing and hosting the conference upon which this volume is based.

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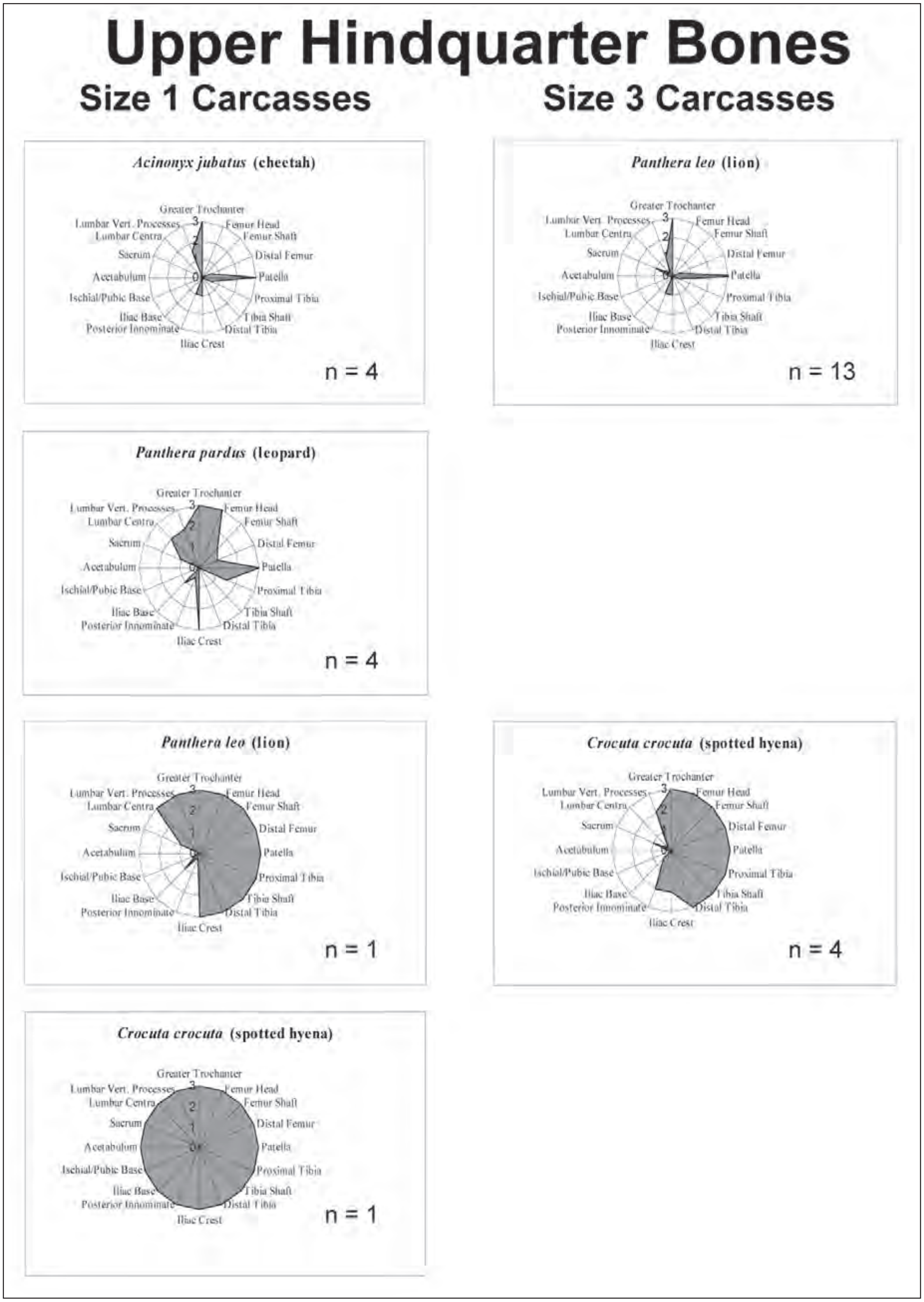
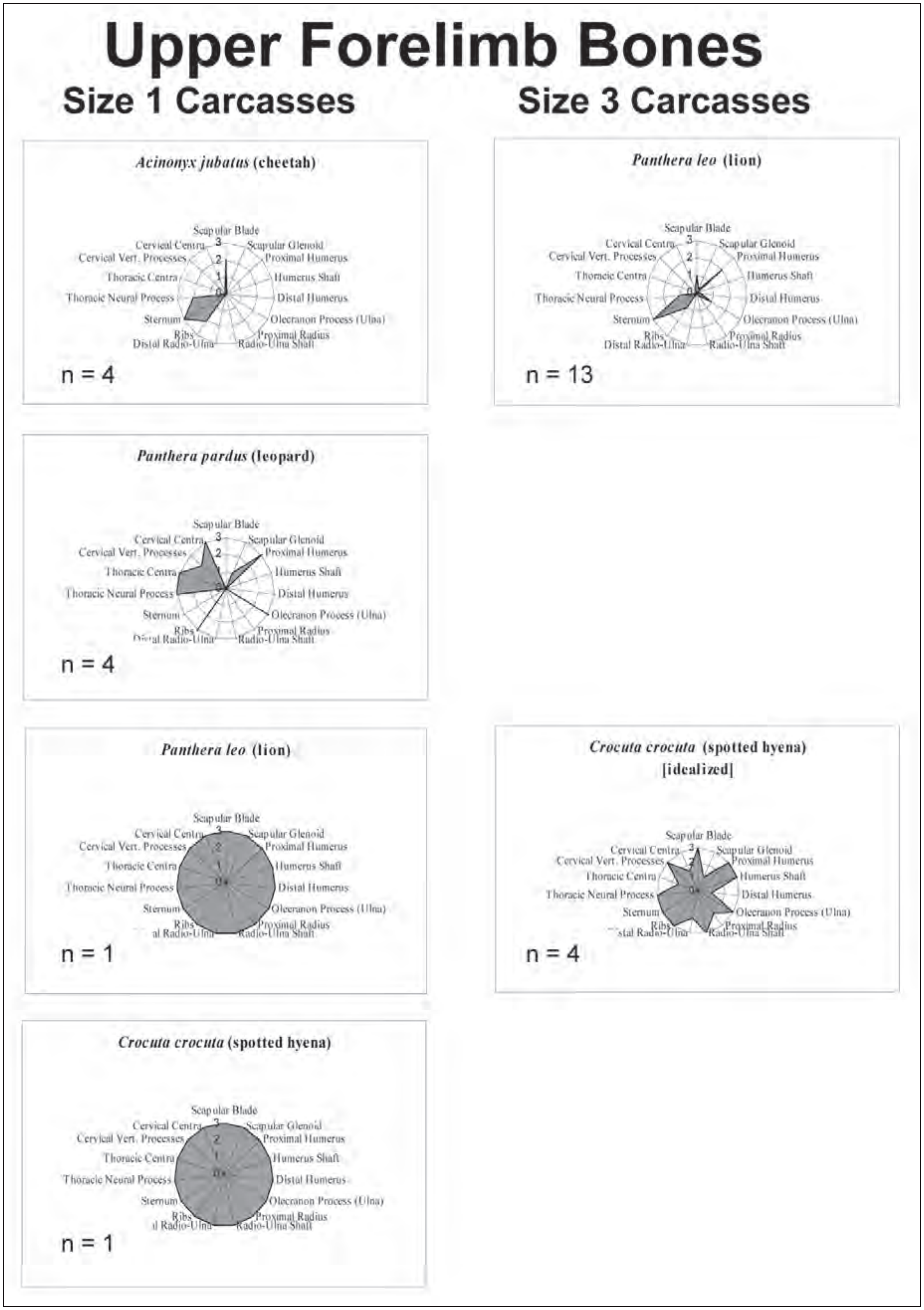


Figure 7. Contrasting degrees of bone damage and destruction caused by four extant carnivore species to upper hindquarters and upper forelimbs of fresh Size Class 1 ungulate carcasses (e.g., Thomson's gazelle), and by two extant species to Size Class 3 carcasses (e.g., wildebeest). Modal values for damage categories are those observed by Blumenschine to have been inflicted on fresh carcasses by the specified carnivore as the exclusive consumer of the carcass in the Serengeti. Sample size refers to the number of carcasses included in each graph. Degrees of bone damage are categorized by numbers 0-3, in order of increasing damage: 0 = no gross damage, though tooth pits and scores are likely to occur; 1 = marginal gnawing (< 50% of portion is removed); 2 = heavy gnawing/fragmentation; 3 = destruction (may leave bone splinters).


Upper Forelimb Bones
Size 1 Carcasses
Size 3 Carcasses
Acinonyx jubatus (cheetah)
n = 4
Panthera leo (lion)
n = 13
Panthera pardus (leopard)
n = 4
Panthera leo (lion)
n = 1
Crocuta crocuta (spotted hyena) [idealized]
n = 4
Crocuta crocuta (spotted hyena)
n = 1
Scapular Blade
Scapular Glenoid
Proximal Humerus
Humerus Shaft
Distal Humerus
Olecranon Process (Ulna)
Proximal Radius
Radio-Ulna Shaft
Distal Radio-Ulna
Ribs
Sternum
Thoracic Neural Process
Thoracic Centra
Cervical Vert. Processes
Cervical Centra
0
1
2
3

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