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Analysis of a bone assemblage made by chimpanzees at Gombe National Park, Tanzania

Chimpanzee hunting provides information on prey characteristics and constraints acting on a large-bodied primate lacking a hunting technology, and has important implications for modeling hunting by fossil hominids. Analysis of the remains of five red colobus monkeys captured and consumed by Gombe chimpanzees in a single hunting bout provides one of the first opportunities to investigate the characteristics of prey bones surviving chimpanzee consumption. Four of the five individuals (an older infant, two juveniles and one subadult) were preserved in the bone assemblage; a neonate was entirely consumed. Cranial and mandibular fragments had the highest survivorships, followed by the scapulae and long bones. Post-cranial axial elements had the lowest survivorships. A high percentage (80%) of the long bones and ribs surviving consumption were damaged, most commonly through crenulation and step fracturing of bone ends. One of two partially reconstructed crania preserves a canine puncture through its left parietal. Proposed characteristics of faunal assemblages formed through chimpanzee-like hunting include small modal prey size, limited taxonomic diversity, a high proportion of immature individuals and a high frequency of skull bones. These characteristics would not uniquely identify hunting by fossil primates in the geological record, necessitating a contextual approach to diagnose hunting by hominids not forming an archeological record.

Hominid utilization of vertebrate tissue is first unambiguously documented at 2·5 m.y.a. Rather than representing a strict "scavenging phase" in the evolution of hominid–prey interactions, Oldowan hominid carnivory may represent the overlay of large mammal scavenging on a tradition of small mammal hunting having a low archeological visibility.

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Introduction

Humans in non-agricultural societies devote a great deal of effort to the acquisition of foods high in protein and fat, including vertebrate prey (Kaplan & Hill, 1985; Bunn *et al.*, 1988; O'Connell *et al.*, 1988; Yellen, 1991). Animal tissue provides a high value currency for sexual negotiation with females, for provisioning of offspring and kin and for reciprocal exchanges (Blurton Jones, 1987; Hawkes, 1991, 1993; McGrew & Feistner, 1992; Hill & Kaplan, 1993). During the course of human evolution, increased consumption of animal tissue fueled brain expansion in the genus *Homo* and may have been intimately associated with the development of a sexual division of labor and paternal investment in mates and offspring (Isaac, 1978; Lovejoy, 1981; McGrew, 1992; Stanley, 1992; Oliver, 1994; Aiello & Wheeler, 1995; Milton, 1999). The documentation of subsistence change in human evolution, including the incorporation of increased quantities of animal tissue, is therefore of concern to paleoanthropologists.

Over the last three decades, research on Oldowan hominid activities has provided unequivocal evidence of hominid utilization of vertebrate tissue by approximately 2·5 Ma (Leakey, 1971; Isaac, 1978; Bunn & Kroll, 1986; Potts, 1988; de Heinzelin et al., 1999). At the same time that faunal utilization by Oldowan hominids was being described, primatologists documented systematic hunting by the nonhuman primate genera Pan, Papio and Cebus (Strum, 1981; Rose, 1997; Uehara, 1997). However, few attempts have been made to assess hominid foraging practices, particularly for animal tissue, in light of data collected by primatologists (Rose & Marshall, 1996). During the course of a five-year study of the predator–prey relationship between chimpanzees (Pan troglodytes) and red colobus monkeys (Colobus badius) at Gombe National Park, Tanzania, one of us (CS) observed 60 hunts in which red colobus were killed. A prey bone assemblage was collected from a kill site following one of these hunts. Here we provide the first detailed description of bones from prey consumed by wild chimpanzees and discuss the implications of this sample for assessing hunting by extinct hominoids. We are particularly interested in encouraging the laboratory and fieldwork necessary to diagnose hominoid hunting in the fossil record prior to the advent of a lithic technology. We hope here to encourage greater interaction between primatologists and paleoanthropologists in framing questions and testing hypotheses about human evolution.

Chimpanzee predation at Gombe

Of the four species of great apes, only chimpanzees (Pan troglodytes) eat meat on a frequent basis, and their hunting patterns and tactics have been the topic of much research. Hunting and meat consumption by wild chimpanzees was first documented in Gombe National Park on the northeastern shore of Lake Tanganyika in the early 1960s (Goodall, 1968, 1986) (Figure 1). Since that time, hunting has been documented in other chimpanzee communities across equatorial Africa (Nishida et al., 1979; Takahata et al., 1984; Boesch & Boesch, 1989; McGrew, 1992; Stanford et al., 1994a; Stanford, 1996, 1998; Mitani & Watts, 1999).

The vegetation at Gombe consists of continuous canopy riparian forest in the valley floors and open woodland to wooded grassland at higher elevations. Open patches of grass are generally only found on top of ridges (Goodall, 1986; Collins & McGrew, 1988). Chimpanzees utilize riparian forest most intensively, but occasionally use more open habitats. Red colobus monkeys compose more than 80% of the Gombe chimpanzees' prey, but other small mammals, including infant and juvenile bushpigs (Potamochoerus porcus) and blue duikers (Cephalophus monticola), are also taken (Goodall, 1986; Stanford et al., 1994a). In addition to its value as a source of protein, fat and micronutrients, animal tissue is shared to form or maintain political bonds and to gain access to sexually receptive females. More than 90% of kills are made by males, and most hunting is carried out in a group context.

Chimpanzee hunting success is positively correlated with party size and the number of adult males in the party (Boesch & Boesch, 1989; Stanford et al., 1994a; Mitani & Watts, 1999), with the largest chimpanzee hunting parties including more than 10 adult males. The decision to hunt at Gombe is related to at least three social factors: overall foraging party size, the number of adult males in the foraging party and the presence of swollen (estrous) females (Stanford et al., 1994b). Although they are mainly frugivorous, and meat composes less than 5% of the diet annually, the amount of vertebrate tissue eaten by wild chimpanzee communities can exceed
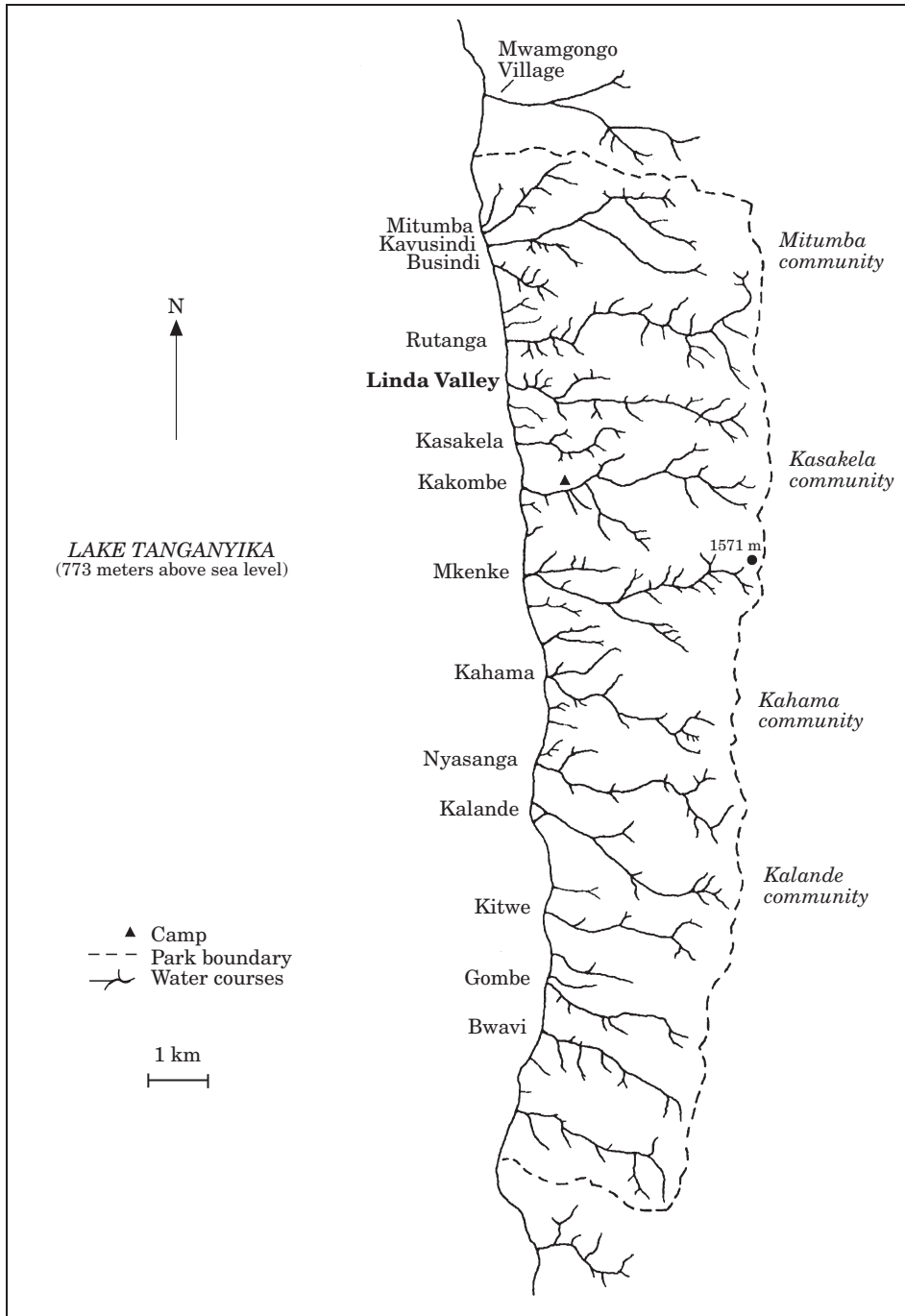
Figure 1. The position of Linda Valley within Gombe National Park, Tanzania. After Goodall (1986:46).

600 kg in some years (Stanford, 1998). Chimpanzee hunting intensity at Gombe varies in relation to patterns of home range use, creating a ''predation landscape'' (Stanford, 1996). Within the predation core area, the impact of hunting on red colobus groups is severe, strongly influencing group size, population size and age structure due to the differential harvesting of immature individuals (Stanford, 1996). The percentage of hunts decreases and red colobus group size increases with distance from the core area.

Hunt yielding the Colobus skeletal sample

On 3 September 1994, at 8:48 a.m., one of us (CS) observed a party of eight chimpanzees, including five adult and adolescent males, as they attacked a group of about 40 red colobus in Linda Valley in Gombe National Park (Figure 1). The low trees and broken canopy gave the monkeys few escape routes, and within 3 min the chimpanzees had captured five red colobus (one neonate, one older infant, two juveniles and one subadult; age classes defined in Stanford, 1998). The combined estimated carcass weight was 12 kg. The alpha male chimpanzee Freud captured one colobus and stole a second carcass from Tubi, who had made his own kill. Other kills were made by adult males Wilkie, Frodo and Prof. The kills were consumed over a $3\frac{1}{2}$-hr period and between 7:00 a.m. and 1:00 p.m. colobus meat was the only food consumed by the chimpanzee party. The kill site occupied three consumption locales with a maximum separation of approximately 25 m. The first locale was underneath the canopy of a large *Parinari curatellafolia* tree, where Freud consumed parts of the juvenile and subadult carcasses that he controlled. He shared some tissue with Tubi, who in turn climbed the tree and shared with Kris. Bones were dropped from the tree by both Tubi and Kris, as well as left on the ground by Freud. Frodo killed a colobus neonate,

which he consumed alone on the ground 8 m to the southeast of Freud's tree. Wilkie and Prof killed an infant and juvenile, respectively, which they consumed on the ground at the third locale, approximately 25 m northeast of Freud's tree. Freud ultimately abandoned one of the two carcasses he controlled (the subadult), after consuming its head, left forelimb and left hindlimb. This carcass was collected for use in a scavenging experiment. As the chimpanzees moved away from the area, the leaf litter at the consumption locales was carefully inspected and 39 bone fragments were collected for analysis. The bones were macerated in vials of water until they were defleshed and degreased and then allowed to air dry.

Analysis of the prey residues

Skeletal part representation

Tables 1 and 2 present the skeletal part representation of the sample, as number of identifiable specimens (NISP), minimum number of elements (MNE) and minimum number of individuals (MNI). NISP is a simple tally of the fragments, MNE is the minimum number of bones needed to account for all of the fragments in the sample and MNI is the minimum number of individuals necessary to account for all of the bones in the sample (Lyman, 1994). Table 3 provides specimen totals and percentage representation of different regions of the colobus skeleton. Table 4 presents bone survivorship data. Figure 2 presents the MNI information in schematic form. Chimpanzees typically entirely consume their prey, including the bones. However, this hunt suggests that under some circumstances (e.g., a large enough quantity of animal tissue to satiate the group) carcasses with some resource life are abandoned. In the following discussion, skeletal part frequencies and bone survivorship are calculated first excluding and then including the

Table 1 Part representation of *Colobus badius* skulls* after consumption by chimpanzees

Skeletal part	Side	NISP	MNE	MNI
Miscellaneous Cranial				
Maxilla with teeth	1L, 2R	2	2	2 (1 older infant, 1 juvenile)
Frontal		1		1
Frontal or parietal fragment		1		1
Zygomatic	R	2		2
Temporal	2L, 1R	3		2
Cranial fragments		3		1
Cranium 1		1	1	1
Frontal				
Parietal	L and R			
Occipital				
Cranium 2		1		1
Parietal	L and R			
Occipital				
Total cranial sample		14	3	3 (1 older infant, 2 juveniles)
Hemimandibles with teeth	3L, 1R	4	4	3 (1 older infant, 2 juveniles)
Total skull sample		18	7	3 (1 older infant, 2 juveniles)
Total proportion of skull sample consisting of gnathic fragments		33·3%	85·7%	

*Cranium 1 and 2 consist of pieces conjoined following cleaning. Note that the original number of skulls was five, but only three are represented in the assemblage. Unless otherwise noted, fragments are from the juvenile age class.

bones of the partial carcass (with a nearly complete axial skeleton and right fore and hindlimbs) abandoned by Freud. In the former case, bone proportions and survivorship provide an indication of which parts are most likely to survive chimpanzee consumption. As discussed below, there tends to be a preservational bias against bones and/or bone parts of low bulk density such as the vertebrae, ribs, innominates and long bone epiphyses (Lyman, 1994).

Since the leaf litter was not swept and sieved, the possibility exists that some small bone fragments were missed. However, the consumption locales were spatially focused and very carefully investigated. It thus seems likely that the collected sample provides a good representation of the bones surviving consumption. As illustrated in Figure 3 and Table 1, a wide variety of cranial parts were preserved, including fragments of frontal, parietal, occipital, zygomatic, temporal and maxillary bones. The colobus skulls were

fragmented as the brains, eyes, major muscles of mastication, neck muscles and tongues were consumed. Two partial juvenile crania (crania 1 and 2; Figure 3) were reconstructed by conjoining vault fragments. A third, older infant cranium is indicated by a right maxillary fragment and a left hemimandible. A nearly complete mandible and palate, almost certainly from a single juvenile individual, was formed by conjoining left and right hemimandibles and maxillae.

A large percentage of the sample surviving consumption is composed of skull fragments, whether calculated using NISP (58·1%) or MNE (36·8%) (Table 3). Moreover, the highest MNI value of three individuals (two juveniles and one older infant) is obtained from the hemimandibles and crania (Table 1). The two juveniles (the complete mandible and palate and one of the two left hemimandibles) have full deciduous dentitions and erupted M_1s,

Table 2 Representation of *Colobus badius* postcranial bones, with and without the bones from the partial subadult carcass missing its skull and left limbs

	Side	NISP without	NISP with	MNE without	MNE with	MNI without	MNI with
Non-skull axial							
Rib	L and R	2	26	2	26	1	2
Cervical vertebra		0	6	0	6	0	1
Thoracic vertebra		0	12	0	12	0	1
Lumbar vertebra		0	7	0	7	0	1
Sacral vertebra		0	3	0	3	0	1
Caudal vertebra		0	26	0	26	0	1
Total axial		2	80	2	80	1 juvenile	2 (1 juvenile, 1 subadult)
Appendicular							
Scapula	R	3 (1 older infant, 2 juvenile)	4	2 (1 older infant, 1 juvenile)	3	2 (1 older infant, 1 juvenile)	3
Clavicle		0	1	0	1	0	1
Innominate		0	2	0	2	0	1
Humerus	L and R	2	3	2	3	1	2
Radius	L and R	2	3	2	3	1	2
Ulna	R	1	2	1	2	1	2
Femur	L	1	2	1	2	1	2
Tibia	L and ?	2	3	2	3	2 (1 juvenile, 1 subadult)	2 (1 juvenile, 1 subadult)
Fibula	R	0	1	0	1	0	1
Total appendicular		11	21	10	20	3 (1 older infant, 1 juvenile, 1 subadult)	3 (1 older infant, 1 juvenile, 1 subadult)
Total postcranial sample		13	101	12	100	3 (1 older infant, 1 juvenile, 1 subadult)	3 (1 older infant, 1 juvenile, 1 subadult)

The atlas vertebra is assumed to have been consumed with the skull and the left clavicle and scapula are assumed to have been consumed with the left arm. Unless noted otherwise, fragments in the "w/o" columns are from the juvenile age class.

Table 3   Specimen totals and percentage representation of different regions of the *Colobus badius* skeleton

	NISP without	NISP with	MNE without	MNE with
Total skull	18	18	7	7
Ribs and vertebrae	2	80	2	80
Total girdle	3	7	2	6
Total long bones	8	14	8	14
Total sample	31	119	19	107
Percentage skull	58·1%	15·1%	36·8%	6·5%
Percentage ribs and vertebrae	6·5%	67·2%	10·5%	74·8%
Percentage girdle	9·7%	5·9%	10·5%	5·6%
Percentage long bones	25·8%	11·8%	42·1%	13·1%

The girdle category includes the scapulae, clavicles and innominates.

while the older infant has a full deciduous dentition and M_1 in its crypt. A large proportion of the skull sample (33·3% using NISP, 85·7% using MNE) is composed of gnathic fragments. In contrast to the skull, the rest of the axial skeleton (when excluding the partial carcass) is poorly preserved (Tables 2 and 3, Figures 2, 4). Two nearly complete ribs (6·5% of the NISP, 10·5% of the MNE) are the only postcranial axial elements surviving consumption.

The appendicular skeleton comprises 35·5% (NISP) or 52·6% (MNE) of the sample (Figures 2, 4; Tables 2 and 3). Three right scapula fragments are preserved. Two of these (one older infant, one juvenile) include the axillary border and part of the blade, while the third (juvenile) fragment preserves the superior angle. The largely complete left humerus includes the proximal metaphysis, midshaft and distal epiphyseal surface, but the unfused distal epiphysis is missing and the proximal end was chewed off. The right humerus is preserved from just inferior to the proximal metaphysis down to and including the distal metaphysis, but the proximal metaphysis and proximal and distal epiphyses are broken away. Two radial shaft cylinders were also recovered. The left radius is preserved from below the proximal metaphysis down to the distal epiphyseal surface, but the unfused distal epiphysis is missing. The right radius and ulna consists of nearly complete diaphyses, missing their proximal and distal ends. The left femoral cylinder is preserved from the proximal end (lacking epiphyses) inferiorly to (but not including) the distal metaphysis. The surface for the greater trochanter epiphysis is broken away, as is approximately one-third of the femoral head epiphyseal surface. The epiphyseal surface for the lesser trochanter is preserved. None of the proximal epiphyses were recovered. The left tibia is complete save for the unfused and missing proximal and distal epiphyses. All of the long bones described up to this point are similarly proportioned and may belong to a single juvenile individual. The last limb bone is a shaft cylinder fragment with a badly offset break, healed antemortem and encased in callus. It is probably a distal tibia from a much larger individual (subadult) than the other postcrania. The fragment is composed of the distal shaft, metaphysis and epiphyseal surface, but lacks the unfused distal epiphysis.

Calculations of bone survivorship provide a further indication of the low representation of postcranial axial parts (Table 4) and the relatively high representation of skull parts.

Table 4 *Colobus badius* bone survivorship, calculated with and without the bones of the partial subadult carcass*

Skeletal part	Observed without carcass (MNE)	Expected without carcass	% survivorship (without carcass)	Observed with carcass (MNE)	Expected with carcass	% survivorship (with carcass)
Cranium	3	5	60·0	3	5	60·0
Hemimandible	4	10	40·0	4	10	40·0
Scapula	2	9	22·2	3	10	30·0
Humerus	2	9	22·2	3	10	30·0
Radius	2	9	22·2	3	10	30·0
Tibia	2	9	22·2	3	10	30·0
Ulna	1	9	11·1	2	10	20·0
Femur	1	9	11·1	2	10	20·0
Ribs	2	96	2·1	26	120	21·7
Cervical	0	29	0·0	6	35	17·1
Thoracic	0	48	0·0	12	60	20·0
Lumbar	0	28	0·0	7	35	20·0
Sacral	0	12	0·0	3	15	20·0
Caudal	0	104	0·0	26	130	20·0
Clavicle	0	9	0·0	1	10	10·0
Innominate	0	8	0·0	2	10	20·0
Fibula	0	9	0·0	1	10	10·0

*The survivorship calculations excluding the partial carcass provide an indication of the skeletal elements most likely to survive chimpanzee consumption. Survivorship was calculated by dividing the observed MNE value of a particular skeletal element by its expected value. Without the partial carcass, the expected value is the number of times a particular skeletal element occurred in the four individuals consumed, with the addition of its occurrence in the portions of the subadult that were eaten (the skull and atlas, left forelimb and pectoral girdle and left hindlimb). For example, the expected value for the cranium is 5 and for the hemimandible is 10, given that the skulls of all five individuals were consumed. The expected value for the humerus is 9, given that both forelimbs of four individuals were consumed, but only the left forelimb of the subadult was eaten. The expected value with the carcass is simply the number of times a skeletal element occurs in five colobus individuals.

Of the bones surviving chimpanzee consumption, survivorship is highest for the cranium (60·0%) and hemimandible (40·0%), lower for the scapula and some long bones (survivorship of 11·1–22·2%) and extremely low for the rest of the axial skeleton (0–2·1%).

In summary, parts of four of the five colobus individuals survived chimpanzee consumption. Skull fragments were derived from the older infant and two juveniles. The postcranial remains, save one scapula (probably from the older infant) and tibia (from the subadult) are possibly from a single juvenile individual [Figures 2(a), 4]. This is again a reflection of the higher survivorship of skull pieces, particularly gnathic fragments. No trace of the neonate killed by Frodo was recovered.

When the bones of the partial carcass are included in the totals, the relative proportions of ribs and vertebrae increase dramatically, up to 67·2% (NISP) and 74·8% (MNE) of the sample (Table 3). However, the increase in the relative proportion of the vertebrae and ribs masks the fact that their survivorship is two to three times lower than the survivorship of the cranium or mandible (Table 4).

There is little documentation in the literature of prey bone representation following chimpanzee consumption. However, a photograph of the remnants of a bushbuck (*Tragelaphus scriptus*) fawn caught and consumed by chimpanzees of the M-group in the Mahale Mountains, Tanzania, was reproduced by Kawanaka (1982; Figure 4, p. 369). This sample consisted of both hemimandibles, a partial scapula and approximately six long bone fragments. The presence of skull and appendicular bones and lack of axial bones is generally similar to the representation of bone fragments recovered in this study. It suggests that ribs and vertebrae rarely survive chimpanzee consumption due to their low structural density (Lyman, 1994).

Bone damage

Recently, Pickering & Wallis (1997) reported on captive chimpanzee mastication damage to goat, cattle and deer long bones and ribs which had been cleaned and coated with food substances. Seventy-four per cent of the recovered bones from their experiments exhibited chimpanzee mastication damage (Table 5). While our sample of long bones and ribs is small ($n=10$), a similar percentage (80%) were damaged during consumption. However, the intensity of damage is not nearly as pronounced in the colobus bone sample, reflecting differences in the actors and consumption setting (captive chimpanzees *vs.* wild chimpanzees), the motivation of the actors (consumption of food coatings off meatless bones *vs.* consumption of whole carcasses) and bone size (relatively large goat, deer and cow bones *vs.* monkey bones). The extensive gnawing damage noted in the captive setting may also reflect ''novelty chewing'' (Pickering & Wallis, 1997) or ''boredom chewing'' (Lyman, 1994) by the chimpanzees. While differences in damage intensity exist, many of the same types of damage were noted in both samples (Table 5; Figure 4). The limb bone sample consists of eight long bone cylinders. Ten of the 16 articular ends (62·5%) had been chewed off, presumably to access grease and marrow in the epiphyses and to allow marrow to be sucked out of the diaphyses. Many of the preserved portions of the long bone ends are crenulated and exhibit step fractures and puncturing or crushing, generated as the chimpanzees loaded the bones with their cheekteeth. Three of the eight long bones exhibited shallow tooth scores, but no pitting was observed.

Both partial crania exhibit chimpanzee tooth damage. Gombe chimpanzees frequently kill immature prey with a bite to the head (Goodall, 1986). In the process of piecing together cranium 2, we observed pitting on both parietals as well as a canine
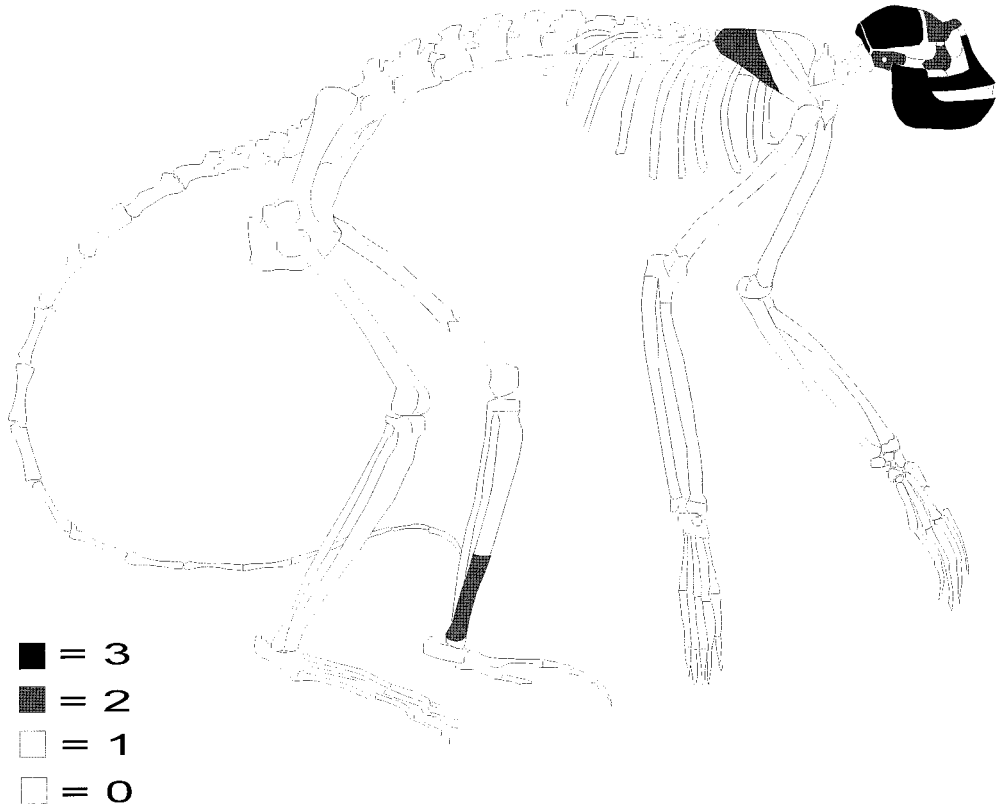
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Figure 2. (a).

puncture mark through the left parietal (Figures 3 and 5). The greatest diameter of the puncture was 10·6 mm. The canine was forced deep into the vault, pushing flakes of bone into its interior. Several isolated pits were also found on the left parietal of cranium 1. The vault bones of both reconstructed crania are cracked and the parietals in particular are deformed laterally and superiorly (i.e., pulled away from the sagittal plane). This deformation probably occurred while accessing the brain.

The conjoining hemimandibles lack only their coronoid processes and condyles (Figure 3). The additional left hemimandibles have a damaged coronoid process and a damaged mandibular angle, respectively. The damage to the condylar region probably occurred when disarticulating the mandibles from the crania, while the damage to the coronoid processes and mandibular angle may have resulted during consumption of the temporalis, masseter and medial pterygoid muscle masses.

Paleoanthropological implications of chimpanzee hunting

Characteristics of faunal assemblages formed through chimpanzee-like hunting
Several lines of evidence suggest that small mammal hunting was common within the Hominidae. Primate hunting, *per se*, is not unusual. The fact that vertebrates are hunted by a diverse array of primate taxa (nine families, 26 genera and 38 species, according to Butynski, 1982) indicates that hominid hunting is not an unreasonable
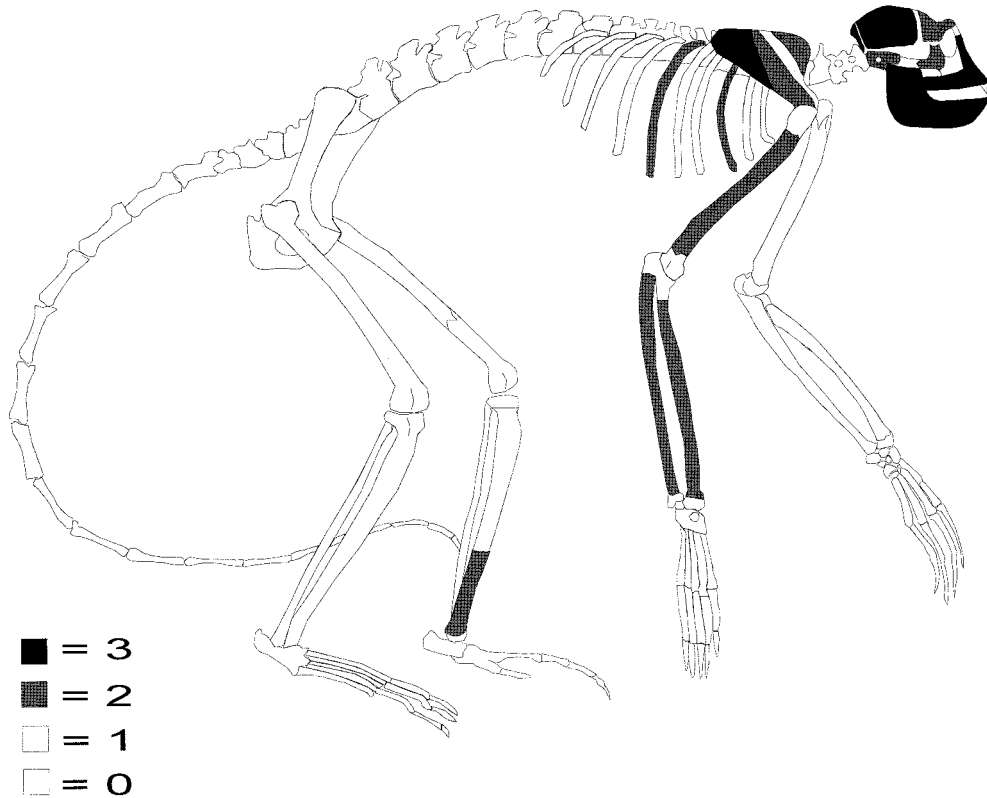
Figure 2. (b).

Figure 2. Colobus skeleton exhibiting sample MNI by anatomical part both without (a) and with (b) the partial subadult carcass abandoned by Freud. Note that the total MNI represented is 4; an older infant and two juveniles based on the skull and a subadult based on a distal tibia fragment and the partial carcass. Colobus skeleton after Kingdon (1974:168).

proposition. A strong argument can be made that hunting is a homologous behavior in chimpanzees and humans (McGrew, 1992; Wrangham *et al.*, 1996; Wrangham & Peterson, 1996). If this is the case, small mammal hunting was likely to have been conducted by all early hominid taxa. This is supported indirectly by evidence that animal tissue was consumed by *Australopithecus africanus*, *Paranthropus robustus*, at least one species of early *Homo* and perhaps *A. garhi* (Sillen, 1992; Bunn & Ezzo, 1993; Lee-Thorp *et al.*, 1994; Oliver, 1994; Aiello & Wheeler, 1995; de Heinzelin *et al.*, 1999; Sponheimer & Lee-Thorp, 1999) and the

strong possibility that *H. ergaster*/early *H. erectus* was a competent predator (Walker, 1984; Shipman & Walker, 1989; Monahan, 1996). Studies of chimpanzee hunting are useful in considering australopithecine predatory behavior by indicating the prey characteristics of a large bodied primate hunting and processing fauna without the benefits of a lithic technology (Stanford, 1996). All nonhuman primates are limited to relatively small, frequently immature prey, which can be easily captured, dispatched, disarticulated and consumed (Strum, 1981; Stanford, 1996; Rose, 1997; Uehara, 1997). Like baboons and
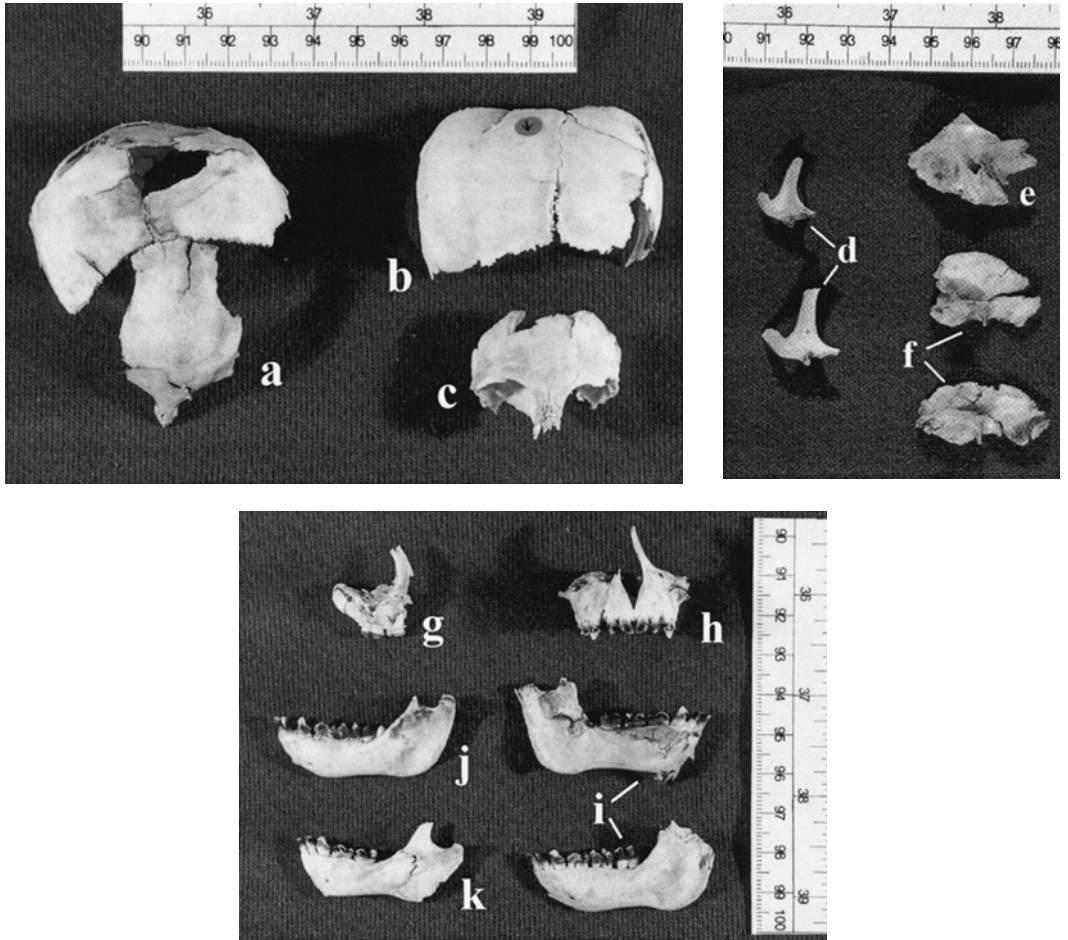
Figure 3. Colobus monkey skull part representation. Unless otherwise stated, all fragments are from juvenile individuals. (a) and (b) are partial crania 1 and 2, respectively, superior aspect. (c) Is a frontal fragment with partial nasal region, frontal aspect, which may belong to cranium 2. (d) Refers to two right zygomatic bones, lateral aspect. (e) Is a right temporal bone, lateral aspect. (f) Refers to two left temporal bones, lateral aspect. (g) Is a right older infant maxilla, lateral aspect. (h) Refers to conjoining left and right maxillae, frontal aspect. (i) Refers to conjoining left and right hemimandibles, lateral aspect. (j) and (k) Are left juvenile and older infant hemimandibles, respectively, lateral aspect.

chimpanzees, it is likely that hominids had favored areas within their ranges, some (perhaps most) reflecting the distribution of plant food resources and sleeping sites (Sept, 1986; Rose & Marshall, 1996). Predation core areas comparable to those seen in Gombe (Stanford, 1996) may have existed in the past. Fossil apes or hominids may have been the primary predators of some small mammal taxa within their core areas. Moreover, predation core areas can be stable over time; for example, the core area of the Kasakela chimpanzee community at Gombe has been stable for three decades (Stanford, 1996). Thus, over geologic time, death assemblages of favoured prey animals may have accumulated.

It is important, then, to diagnose a set of criteria allowing the recognition of chimpanzee-like hunting behavior in the
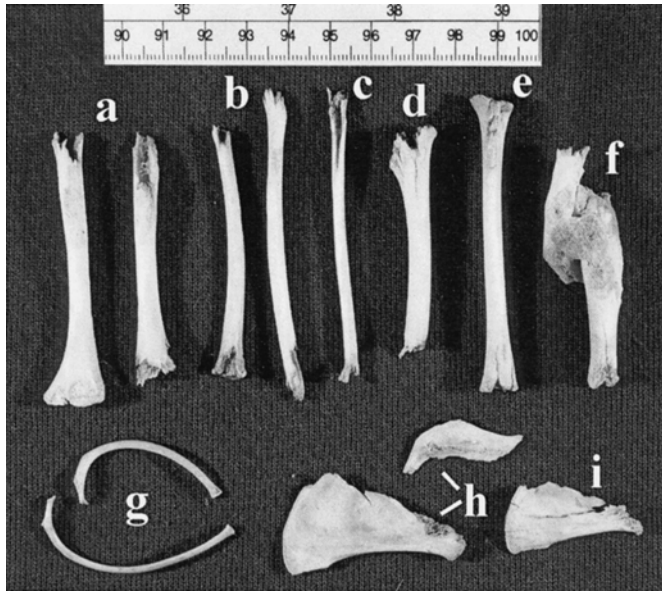
Figure 4. Colobus monkey postcranial part representation. All bones except (h) and (i) are shown in anterior aspect. The latter bones are shown in dorsal aspect. Unless otherwise stated, all fragments are from juvenile individuals. (a) and (b) Refer to left and right humeri and radii, respectively. (c) Is a right ulnar shaft. (d) Is a left femur. (e) Is a left tibia. (f) Is a subadult tibia(?) shaft with a badly offset break. (g) Refers to left and right ribs. (h) Refers to scapular blade and superior angle fragments, while (i) is an older infant scapular blade fragment.

Table 5 The percentage of damaged colobus long bones and ribs, compared to the damage inflicted on bovid and cervid long bones and ribs by captive chimps

Chimpanzee group	Types of bone damage						
	Crenulation	Step fractures	Peeling	Pits	Scores	Notches	Punctures/crushing
Gombe (*n*=10)	60·0	40·0	10·0	0·0	30·0	10·0	30·0
Captive group							
SRA (*n*=1)	0·0	0·0	0·0	100·0	100·0	0·0	0·0
SRB (*n*=20)	59·1	36·4	27·3	72·7	68·2	18·2	9·1
SRC (*n*=10)	70·0	20·0	50·0	80·0	80·0	20·0	10·0
TU (*n*=31)	20·5	7·7	5·1	33·3	38·5	7·7	10·3

After Pickering & Wallis, 1997, Table 2.

fossil record. Chimpanzee-like hunting would be expected to produce death assemblages with the following characteristics:

(1) *Small modal prey size with a maximum prey weight of approximately 10 kg.* Chimpanzees are limited to prey items

that they can pursue, capture, kill, disarticulate and consume without technological assistance. Presumably this was also true of fossil hominids lacking a hunting and butchering technology. At three localities where chimpanzee hunting has been well documented (Gombe & Mahale in
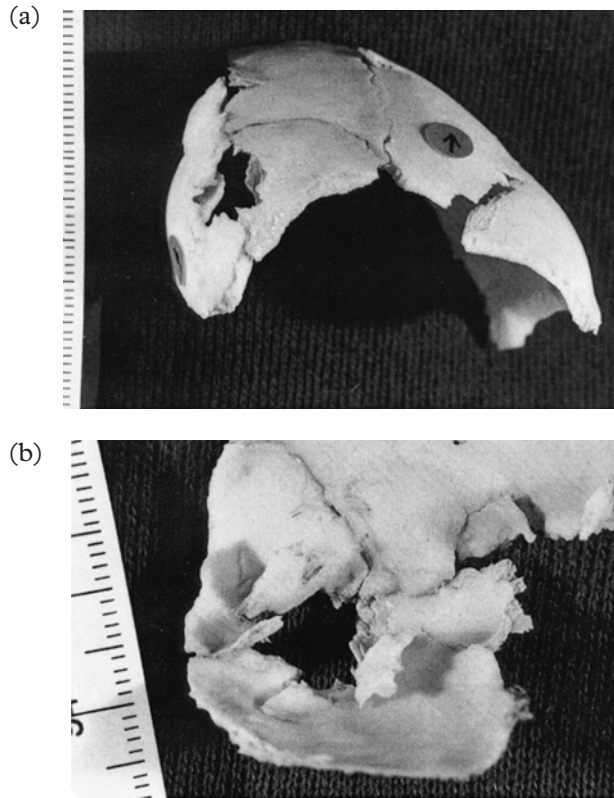
Figure 5. Canine puncture through left parietal of partial cranium 2, external (a) and internal (b) aspects. Arrows on stickers denote pitting by chimpanzee teeth.

Tanzania, Tai in the Ivory Coast) modal prey size ranges between 1 and 5 kg (Boesch & Boesch, 1989; Stanford, 1996; Uehara, 1997) and the largest prey (adult male red colobus) rarely exceeds 10 kg (Smith & Jungers, 1997). Vertebrates commonly consumed by baboons (*Papio anubis* and *P. cynocephalus*) also weigh well under 10 kg (Hausfater, 1976; Strum, 1981; Strum & Mitchell, 1987).

(2) *Limited taxonomic diversity.* At least 32 species of mammals from 12 study sites have been recorded as chimpanzee prey (Uehara, 1997). These include 18 species of primates, as well as rodents and two species each of swine and antelope. There are dif-

ferences in prey selectivity among the best studied communities (e.g., Tai chimpanzees do not hunt blue duikers and bush pigs, while chimpanzees at Gombe and Mahale do), but chimpanzees tend to focus heavily on group-living, arboreal monkeys, particularly red colobus (Uehara, 1997). Red colobus make up 50% or more of the total prey sample in each of the best known chimpanzee communities (Mitani & Watts, 1999). Such selectivity is not uncommon in carnivores [e.g., up to 91% of the prey of cheetahs (*Acinonyx jubatus*) in the Serengeti, Tanzania are Thomson's gazelles (*Gazella thomsoni*)] and almost certainly reflects the interplay of preferred prey size, prey density in the

environment and prey availability to the predator in question (e.g., Kruuk & Turner, 1967; Pienaar, 1969; Schaller, 1972; Bailey, 1993; Caro, 1994). Red colobus are small-bodied (5·46–12·3 kg, Smith & Jungers, 1997), make up a high proportion of the mammalian biomass in woodlands and forest, are frequently found in large groups (mean group size of 28 individuals at Gombe), are commonly encountered during foraging, and at least in East Africa, always include vulnerable, immature individuals in their groups due to aseasonal breeding (Stanford, 1995). A high frequency of predation on a small number of commonly encountered taxa is also the norm for baboons, which focus on Cape hares (*Lepus capensis*) and neonate Thomson's gazelles at Gilgil, Kenya (Strum & Mitchell, 1987) and vervet monkeys (*Cercopithecus aethiops*), hares and neonate gazelles at Amboseli, Kenya (Altman & Altman, 1970; Hausfater, 1976). If Pliocene hominids hunted, they may have focused their attention on small, terrestrial mammals (e.g., young antelopes) rather than the arboreal, group-living monkeys favoured by chimpanzees.

(3) *High proportion of immature individuals.* Immature individuals comprise at least 50% of all prey at Tai and 79% or more at Mahale and Gombe (Boesch & Boesch, 1989; Stanford, 1996; Uehara, 1997). Baboons also frequently hunt immature animals (Strum & Mitchell, 1987), but prey demographics are not available.

(4) *High frequency of skull bones.* The cranium and hemimandibles would have the highest survivorship, followed by appendicular elements. The postcranial axial bones would have the lowest survivorship (Table 4). Given the small size and relative immaturity of the prey in question, this pattern might hold independent of prey species (for example in both monkeys and young antelopes; Kawanaka, 1982). However, skeletal part survivorship would probably vary by broad taxonomic group with slightly larger prey (e.g., vertebrae from 30 kg bovids are more likely to survive carnivore consumption than vertebrae from 30 kg baboons; Brain, 1981).

Suggestions for future research

While helpful in attempting to identify primate hunting in fossil contexts, criteria such as these probably would not uniquely distinguish fossil assemblages formed through chimpanzee-like predation from those formed by other processes. For example, an assemblage lacking vertebrae and ribs can result from a variety of processes. In many mammals there is a negative correlation between the structural density and nutritional value of a particular skeletal part (Lyman, 1994). Thus, different predator taxa consuming a particular prey taxon are going to be attracted to, and more likely to damage or destroy, bones of high food utility. These same skeletal parts, because they generally have low structural densities, are also more prone to destruction through non-behavioral, density-mediated processes such as sediment compaction. Moreover, different actors are likely to produce grossly similar types of damage to bone, simply because of bone's inherent mechanical and structural properties (Hill, 1980; Bunn, 1989; White, 1992).

We believe hominoid hunting can be most fruitfully investigated by combining contextual information with a configurational approach to bone damage. Detailed contextual studies are necessary to document the abiotic and biotic factors involved in the formation of the fossil assemblages under investigation, the relative

representation of different paleohabitats and for accurate paleocommunity recon- structions (Behrensmeyer & Hill, 1980; Behrensmeyer et al., 1992). The paleoeco- logical information assists in identifying small taxa sharing characteristics with chim- panzee prey, for example common occur- rence and the likelihood of overlap in habitat use with the ape or hominid under investi- gation. The remains of potential prey taxa could then be assessed for diagnostic dam- age linking them to a particular predator. We agree with Pickering & Wallis (1997) that a configurational approach may allow for the identification of hunting by Miocene apes and Pliocene hominids. Such an approach seeks to identify the actor from the morphology and location of damage on individual bones as well as the pattern of damage across a bone assemblage (Binford, 1981; Bunn & Kroll, 1986). The necessary datasets are incompletely developed and can only be derived through close interdisci- plinary collaboration. More attention needs to be paid to the order and manner in which wild chimpanzees consume different body regions of their prey and to the systematic collection and description of prey residues. As the skeletal sample of chimpanzee prey increases, it may be possible to determine whether damage patterns diagnostic of chimpanzee, and by extension fossil hominoid, consumption exist (see Pickering & Wallis, (1997) for a discussion of the appropriateness of a chimpanzee model). This will necessitate collecting equivalent data from African avian and mammalian carnivores consuming similarly-sized prey, building on the work of Brain (1981) and Andrews (1990). Feeding experiments with captive chimpanzees and carnivores to better diagnose their respective damage patterns under controlled conditions would also be useful. This would allow researchers to modify variables such as group size, composition and actor motivation. It would be particularly informative if the feeding experiments of Pickering & Wallis (1997) could be extended to include meaty car- casses rather than cleaned bones coated with food substances. Finally, continued paleodi- etary research should assist in determining whether specific fossil hominoid taxa were consuming substantial quantities of animal protein (e.g., *A. africanus* and *P. robustus*; Sillen, 1992; Lee-Thorp et al., 1994; Sponheimer & Lee-Thorp, 1999). Potential prey taxa of these hominoid species could then be targeted for detailed configurational investigation.

Discussion

Small mammal predation by chimpanzees not only provides a framework for consider- ing carnivory in hominids lacking a lithic technology, it also provides a useful perspective for considering debates over the behavior of hominids forming the earliest archeological sites, usually attributed to the Oldowan Industrial Complex (Isaac, 1984). There is general agreement that Oldowan hominids consumed larger amounts of ani- mal tissue than living nonhuman primates, that they had early access to up to gazelle- sized mammals [Potts' (1988) very small and small size classes, <72 kg], that they generally acquired animals larger than this through scavenging, that their utilization of large mammal carcasses increased their con- tact and competition with large carnivores and that they transported both stone tools and carcass parts over long distances relative to nonhuman primates (Isaac, 1978; Bunn & Kroll, 1986; Potts, 1988; Cavallo & Blumenschine, 1989; Schick & Toth, 1993; Oliver, 1994; Rose & Marshall, 1996; Capaldo, 1997; Dominguez-Rodrigo, 1997; Selvaggio, 1998). However, there is little consensus on the frequency or scale of faunal utilization or the dominant mode of carcass acquisition.

Frequently, debate on the mode of carcass acquisition has focused on whether

Oldowan hominids were primarily scavenging or hunting prey, and if they were scavenging whether it was active or passive (Binford, 1981; Bunn & Kroll, 1986; Shipman, 1986; Blumenschine, 1987, 1995; Potts, 1988; Blumenschine & Marean, 1993; Bunn & Ezzo, 1993; Capaldo, 1997; Selvaggio, 1998). As has been noted elsewhere (e.g., Bunn & Ezzo, 1993; Tooby, 1987), the scavenging *vs.* hunting dichotomy oversimplifies and rigidly defines what is likely to have been a complex, flexible foraging strategy. Moreover, it presupposes that scavenging and hunting would be equally visible in the archeological record. This seems unlikely, given the taphonomic biases acting on the animals most likely to have been hunted (i.e., small mammals) versus those most likely to have been scavenged (i.e., medium and large mammals) and potential differences in transport behavior based on carcass size (Lupo, 1998; Lyman, 1994; Monahan, 1998). Convincing evidence for Oldowan hominid utilization of a very small (<1 kg) mammal (the extinct hedgehog *Erinaceus broomi*) which was almost certainly hunted has recently been published (Fernandez-Jalvo *et al.*, 1999). This suggests that minimally, Oldowan hominids were hunting prey within the size range of animals hunted by extant nonhuman primates (i.e., <10 kg) and were scavenging the carcasses of animals larger than about 72 kg [Potts' (1988) medium to very large size classes].

The scavenging of large mammal carcasses by Oldowan hominids is a clear departure from the use of vertebrate tissue by nonhuman primates. Scavenging is extremely uncommon, and in chimpanzees, baboons, and capuchins largely consists of pirating freshly killed prey from other group members. Chimpanzees have also pirated fresh kills made by baboons (Morris & Goodall, 1977). The reluctance of baboons and chimpanzees to scavenge tissue from animals they had not killed or had not seen killed (Hasegawa *et al.*, 1983; Strum, 1983; Muller *et al.*, 1995) may have an evolutionary basis. Unlike large mammalian carnivores who routinely scavenge, primates do not have physiological mechanisms to deal with diseases directly transferable from carcass to consumer (Hamilton & Busse, 1978; Ragir & Tiesno, 1996). An aversion to carrion is probably an adaptive means to avoid disease from tainted meat and/or to avoid predators drawn to large mammal carcasses (Hamilton & Busse, 1978; Strum, 1983; Nishida, 1994).

Rather than Oldowan behavior representing a "scavenging phase" in the evolution of hominid–faunal interactions, it seems more likely to us that a tradition of large mammal scavenging developed in hominid communities that already hunted small mammals and valued vertebrate tissue. This would reflect an expansion of the prey search image to recognize large mammal carcasses as well as small game as valuable resources. It has been argued that climatic conditions in Africa became cooler, drier and more variable during the late Pliocene (Vrba, 1985; Potts, 1996; Behrensmeyer *et al.*, 1997). The relaxation of scavenging inhibitions as documented in Oldowan faunal utilization may have been a response to fluctuations in plant food availability and carcass encounter rates seasonally (Blumenschine, 1987; Foley, 1987) and/or over geologic time (Potts, 1998).

Conclusions

The following points can be drawn from this study.

(1) Bones from chimpanzee prey occasionally survive consumption. In the small sample described here, skull fragments have the highest survivorship, while vertebrae and ribs have the lowest survivorship.

(2) Over time, prey residues from hominoid hunting bouts might accumulate in the fossil record, particularly if the hominoid in question was one of the primary predators in its paleo-community, and if predation core areas existed. Assuming minimal taphonomic influences following bone discard, assemblages formed through chimpanzee-like hunting would exhibit limited taxonomic diversity, would be dominated by small taxa and would contain a high proportion of immature individuals and a high frequency of skull bones.

(3) A combination of contextual studies and a configurational approach to assessing bone damage may allow for the identification of hunting by Miocene apes and/or Pliocene hominids. However, actualistic experiments and field observations of chimpanzees and carnivores consuming small prey need to be carried out in order to confidently diagnose hunting by fossil primates.

(4) Hunting by nonhuman primates is relatively common, while scavenging rarely occurs, probably due to attendant health and predation risks. Indirect evidence suggests that small mammal hunting was common within the Hominidae.

(5) Oldowan hominid faunal utilization may have developed through the expansion of a small mammal hunting tradition to include scavenged tissue from large mammal carcasses. The impetus for the utilization of scavenged tissue may have been a fluctuating resource base both seasonally and over geologic time during the late Pliocene.

(6) The weight placed on scavenging in recent discussion of Oldowan hominid foraging ecology may overemphasize one component of what was probably a flexible strategy including both hunting and scavenging.

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