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Taphonomic analysis of skeletal remains from chimpanzee hunts at Ngogo, Kibale National Park, Uganda

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Abstract

This study provides a taphonomic analysis of the largest known sample of bone fragments collected from chimpanzee hunts. The entire sample consists of 455 bone fragments from 57 chimpanzee hunting episodes of 65 prey individuals at Ngogo, Kibale National Park, Uganda. It has low taxonomic diversity, consisting overwhelmingly of primates, especially red colobus monkeys. The age distribution of the prey remains is skewed towards pre-adults. Cranial bones are the dominant element, followed by long bones. Axial postcranial elements have low survivorship, with a complete absence of pre-caudal vertebrae. Bone is damaged in distinct ways, such as: destruction of long bone ends, typically with intact but chewed shafts; fragmentation and compression cracking of crania; and preservation of only the iliac blades of the innominates. Tooth marks are present but uncommon (4.4% of total NISP).

These analyses enable us to: 1) describe and characterize consistent patterns of bone damage inflicted by chimpanzees across a much larger prey sample than has been previously studied; 2) make a preliminary comparison of the generalized chimpanzee taphonomic signature to that of leopard and eagle consumption of primates, as well as modern human consumption of small mammals; and 3) assess the utility of such samples for recognition of early hominin small mammal carnivory. We present a model that may be useful for detecting a pre-technological hominin carnivory and suggest some fossil locales at which close inspection of cercopithecoid remains for the above patterns might reveal traces of hominin hunting, though we caution that a pre-technological hominin hunted ''assemblage'' is not likely to be archaeologically visible.

Keywords: Hunting; Taphonomy

Introduction

Studies of chimpanzee hunting behavior in the wild have yielded considerable information about prey selection and hunting participation, frequency, and success (e.g., Uehara, 1997; Stanford, 1998; Mitani and Watts, 1999; Boesch and Boesch-Achermann, 2000; Watts and Mitani, 2002). Chimpanzees hunt vertebrate prey everywhere that they have been studied in any detail (Uehara, 1997; Table 1). While 38 species of nonhuman primates hunt and/or eat vertebrate prey, only chimpanzees and baboons hunt in groups, stalk their prey, and share meat (Strum, 1981, 1983; Butynski, 1982; Boesch and Boesch, 1989; Stanford, 1998; Mitani and Watts, 1999). The close evolutionary relationship between chimpanzees and humans, as well as anatomical and possible niche similarities, provides the rationale for using chimpanzee predatory behavior to model the hunting ecology and behavior of pre-technological hominins (e.g., Stanford, 1996, 1999).

Little is known about prey remains from chimpanzee hunts. Analyses of such remains might provide insights into potential early hominin prey remains in the paleontological record. Observations of chimpanzee predation at the Mahale Mountains made note of bone refuse, but this was not systematically

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Table 1
Mammalian species eaten by chimpanzees

Family	Species	Location	Country	Chimp species
Insectivora	*Rhynchocyon cirnei*	Mahale	Tanzania	*P.t schweinfurthii*
		Budongo	Uganda	*P.t.schweinfurthii*
Rodentia	*Cricetomys emini*	Mahale	Tanzania	*P.t schweinfurthii*
	Thryonomys swinderianus	Mahale	Tanzania	*P.t schweinfurthii*
	Protoxerus and/or *Heliosciurus*	Mahale	Tanzania	*P.t schweinfurthii*
	Funisciurus sp.	Gombe	Tanzania	*P.t schweinfurthii*
	Unidentified small mouse or rat	Gombe	Tanzania	*P.t schweinfurthii*
	Squirrel	Kahuzi-Biega	Congo	*P.t schweinfurthii*
	Flying squirrel (Anomaluridae sp.)	Nouabale-Ndoki	Congo	*P.t.troglodytes*
	Anomalurus derbianus	Tenkere	Sierra Leone	*P.t.verus*
	Rat	Taï	Ivory Coast	*P.t.verus*
	Anomalurus sp.	Wamba and Lilungu	Congo	*P. paniscus*
	Unidentified large squirrel	Lomako	Congo	*P. paniscus*
Pholidota	Pangolin?	Nouabale-Ndoki	Congo	*P.t schweinfurthii*
	Manis tricuspis	Bossou	Guinea	*P.t.verus*
Chiroptera	*Eidolon* sp.	Lilungu	Congo	*P. paniscus*
Hyracoidea	*Heterohyrax brucei*	Mahale	Tanzania	*P.t schweinfurthii*
Artiodactyla	*Cephalophus monticola*	Mahale	Tanzania	*P.t schweinfurthii*
		Budongo and Kibale	Uganda	*P.t schweinfurthii*
		Lope	Gabon	*P.t schweinfurthii*
	Cephalophus callipygus	Kibale	Uganda	*P.t.schweinfurthii*
	Cephalophus sp.	Tenkere	Sierra Leone	*P.t.verus*
		Nouabale-Ndoki	Congo	*P.t.troglodytes*
		Lomako	Congo	*P. paniscus*
	Tragelaphus scriptus	Gombe and Mahale	Tanzania	*P.t schweinfurthii*
	Potamochoerus porcus	Gombe and Mahale	Tanzania	*P.t schweinfurthii*
		Kibale	Uganda	*P.t.schweinfurthii*
	Phacochoerus aethiopicus	Mahale	Tanzania	*P.t schweinfurthii*
Carnivora	*Bdeogale*, *Mungos*, *Ichneumia* sp.	Mahale	Tanzania	*P.t schweinfurthii*
	Viverra civetta	Mahale	Tanzania	*P.t schweinfurthii*
Primates	*Procolobus badius*	Gombe and Mahale	Tanzania	*P.t schweinfurthii*
		Kibale	Uganda	*P.t schweinfurthii*
		Nouabale-Ndoki	Congo	*P.t.troglodytes*
		Taï	Ivory Coast	*P.t.verus*
	Colobus guereza	Budongo and Kibale	Uganda	*P.t schweinfurthii*
	Colobus polykomos	Taï	Ivory Coast	*P.t.verus*
		Tenkere	Sierra Leone	*P.t.verus*
	Colobus satanus	Lope	Gabon	*P.t.troglodytes*
	Procolobus verus	Taï	Ivory Coast	*P.t.verus*
	Cercopithecus mitis	Gombe and Mahale	Tanzania	*P.t schweinfurthii*
		Budongo and Kibale	Uganda	*P.t schweinfurthii*
		Kahuzi-Biega	Congo	*P.t schweinfurthii*
	Cercopithecus ascanius	Kasakati, Gombe and Mahale	Tanzania	*P.t schweinfurthii*
		Kibale	Uganda	*P.t schweinfurthii*
	Chlorocebus aethiops	Mahale	Tanzania	*P.t schweinfurthii*
	Cercopithecus lhoesti	Kahuzi-Biega	Congo	*P.t schweinfurthii*
	Cercopithecus cephus	Nouabale-Ndoki	Congo	*P.t.troglodytes*
	Cercopithecus pogonias	Nouabale-Ndoki	Congo	*P.t.troglodytes*
	Cercopithecus diana	Taï	Ivory Coast	*P.t.verus*
	Cercopithecus campbelli	Tankere	Sierra Leone	*P.t.verus*
	Lophocebus albigena	Kibale	Uganda	*P.t.schweinfurthii*
		Lope	Gabon	*P.t.troglodytes*
	Cercocebus atys	Taï	Ivory Coast	*P.t.verus*
	Papio anubis	Gombe	Tanzania	*P.t.schweinfurthii*
		Kibale	Uganda	*P.t.schweinfurthii*
	Galago crassicaudatus	Mahale	Tanzania	*P.t.schweinfurthii*
	Galago senegalensis	Mahale	Tanzania	*P.t.schweinfurthii*
		Mt. Assirik	Senegal	*P.t.verus*
	Perodicticus potto	Taï	Ivory Coast	*P.t.verus*
		Mt. Assinik	Senegal	*P.t.verus*

Data from Uehara, 1997; Mitani and Watts, 1999; Newton-Fisher et al., 2002.

recorded (Nishida et al., 1979; Kawanaka, 1982; Takahata et al., 1984). More recent work documented: 1) bone modification inflicted by captive chimpanzees on bovid and cervid bones (Pickering and Wallis, 1997: hereafter called the "captive" sample); 2) damage to bones found in chimpanzee feces at Kibale National Park (Tappen and Wrangham, 2000: the "fecal" sample); and 3) the bony remains of five red colobus monkeys captured in a single hunting bout at the Gombe National Park (Plummer and Stanford, 2000: the "Gombe" sample).

The most comparable of these studies to the hunting behavior of pre-technological hominins is the Gombe sample. Plummer and Stanford (2000) found that crania and mandibles had high survivorship, followed by scapulae and long bones. They observed a high proportion of crenulation and step fracturing on long bones and ribs, and a tooth puncture in one of the cranial specimens. As we will outline, their descriptions of chimpanzee-hunted faunal assemblages are similar to ours: small prey size, low taxonomic diversity, a focus on immature individuals, and a high frequency of skull bones. Our study supports all of these observations with a much larger sample size.

Chimpanzees of the Ngogo community, Kibale National Park, Uganda, hunt frequently and are unusually successful predators compared with chimpanzees at other sites (Mitani and Watts, 1999; Watts and Mitani, 2002). The frequency and success of hunting by chimpanzees at Ngogo furnish an especially good opportunity to collect bones modified by predation. In this paper, we describe the species composition, age distribution, skeletal element distribution, and bone damage patterns of a very large sample of prey remains from Ngogo. The bone assemblage we analyze here is the largest chimpanzee-hunt refuse collection assembled to date. Our results permit us to make generalizations about what chimpanzees do to prey remains, compare these results to those from other small mammal predators, and speculate about the utility of these remains for recognizing small mammal hunting by early hominins.

Materials and methods

Study site and subjects

At an altitude of about 1400 meters above sea level, Ngogo (Kibale National Park, Uganda) lies at an interface between lowland and montane rainforest. Old growth forest, characterized by a continuous canopy 25–30 meters high, covers most of the Ngogo community territory, but human disturbance has created some spots of regenerating forest and grassland. At Ngogo, chimpanzees live sympatrically with six other common diurnal primates who form their primary prey (Table 2). These include two colobines (*Procolobus badius* and *Colobus guereza*) and four cercopithecines (*Cercopithecus ascanius*, *Cercopithecus mitis*, *Lophocebus albigena*, and *Papio anubis*). Three artiodactyls (*Cephalophus monticola*, *Cephalophus callipygus*, and *Potamochoerus porcus*) are frequently encountered at Ngogo and represent additional potential prey for chimpanzees there.

The Ngogo chimpanzee community is extremely large and included approximately 150 individuals between 1997–2004, when behavioral observations and bone collections were conducted. Like chimpanzees at other sites, the Ngogo chimpanzees form temporary parties that fluctuate in size. While mean party size at Ngogo is 10 individuals (Mitani et al., 2002), chimpanzees there congregate in much larger parties when they hunt monkeys (mean = 24, SD = 9; Mitani and Watts, 1999).

Sample collection and bone identification

Bone fragments were collected at Ngogo by J.C.M. and colleagues while conducting behavioral observations of chimpanzees. Observers in the field recorded the date of the chimpanzee kill, prey species, relative age, and where possible, the sex of the species being consumed. The chimpanzee that made the kill and all others who participated in the consumption of the animal were noted. The remains were collected after the chimpanzees had finished eating and had discarded the bone fragments on the ground. Although fragments of small bones like phalanges and caudal vertebra may have escaped detection, efforts were taken to collect the bones as thoroughly as possible.

The entire sample was divided into two sub-samples collected between 1997–2001 and 2002–2004, respectively. Taxonomic and skeletal element identifications for some bones were done in the field. Bone fragments from the 1997–2001 sub-sample were identified by B.L.P. with the assistance of S. C. Antón using modern primate comparative material at Rutgers University. Bone fragments from the 2002–2004 collection were identified by J.D. by comparing the bones to

Table 2
Diurnal primate species killed by chimpanzees at Ngogo

Species name	Common name	Density at Ngogo, Kibale National Park (groups/km^2)	Number of observed kills (1995–1998)[+]	Number of individuals present in this bone assemblage (1997–2004)
Pan troglodytes	Chimpanzee	n/a	1 (infanticide)	1
Papio anubis	Olive baboon	0.63	1	1
Colobus guereza	Black and white colobus	0.55	11	3
Procolobus badius	Red colobus	2.92	258	58
Cercopithecus ascanius	Red-tailed monkey	6.23	10	5
Cercopithecus mitis	Blue monkey	0.08	1	0
Lophocebus albigena	Gray-cheeked mangabey	2.76	1	0

Data from Uehara, 1997; Mitani and Watts, 1999; Watts and Mitani, 2002; Sanders et al., 2003.
[+] In addition, 10 ungulates and one guinea fowl were killed during this time.

Table 3
Bone modification identification criteria

Type of bone modification	Description/identification criteria	Reference
Mashed edges/ragged-edged gnawing or chewing/ crenulated edges*	Uneven, irregular, jagged edges of long bones caused by intense, sustained chewing, resulting in destruction of epiphyses	Binford, 1981: 51 Brain, 1981: 71–72 Maguire et al., 1980: 79–80 Lyman, 1994: 206–7 Fisher, 1995: 30 Pickering and Wallis, 1997: 1118 (photograph in Pickering and Wallis, 1997: 1119, Fig. 1)
Step fractures	Static loading causes fracture fronts to "jump" when they contact pre-existing split line cracks on bone cortices	Binford, 1981 Shipman et al., 1981 Johnson, 1985: 184 Marshall, 1989 Pickering and Wallis, 1997: 1118 (photograph in Pickering and Wallis, 1997: 1120, Fig. 2)
Peeling back of cortical layers	Ragged, uneven surface with stepped layers of lamellae; can be similar to weathering damage stages 1 and 2 (Behrensmeyer, 1978) but does not cause flaking of cortical bone layers and does not cause cracking parallel to the fiber of the bone structure; individuals strips of bone are grasped between incisors and pulled	White, 1992: 140–143 Pickering and Wallis, 1997: 1119 (photograph in Pickering and Wallis, 1997: 1121, Fig. 3)
Fraying	Crushed and cracked edges with a fringed appearance caused by heavy mastication and probably accompanying slight dissolution from sucking; similar to crenulated edges but 1) more likely to occur on smaller, thinner bones, 2) resulting in deeper longitudinal fissures emanating from bone edges towards center of bone, 3) often with thin bone "peninsulas" jutting out at a parallel or oblique angle to the rest of the bone (see Figs. 11 and 12)	Tappen and Wrangham, 2000: 227 (photograph in Tappen and Wrangham, 2000: 227, Fig. 7)
Tooth pits or punctures	Circular to oval in plan form; crushed internal surface; decreasing diameter as depth from bone surface increases. Punctures (versus pits) occur when bone collapses under pressure of teeth, often with flakes of the outer wall of the bone pressed into the puncture	Maguire et al., 1980 Binford, 1981 Blumenschine and Selvaggio, 1988: 763 Lyman, 1994: 206 Blumenschine et al., 1996: 496 Tappen and Wrangham, 2000: 226
Tooth scores, striations, gouge marks, scratches**	Short to elongated grooves; high breadth:depth ratio; shallow U-shaped cross section; crushed internal surface; usually linear or straight and perpendicular or transverse to the long axis of the bone. Tooth scores occur when a tooth is dragged along the surface of a bone leaving this elongated indentation	Maguire et al., 1980: 79–80 Haynes, 1980, 1983 Binford, 1981: 44–48 Bunn, 1981 Potts and Shipman, 1981 Shipman, 1981: 365 Shipman and Rose, 1983 Eickhoff and Herrmann, 1985 Lyman, 1994: 210 Blumenschine et al., 1996: 496 Tappen and Wrangham, 2000: 226
Tooth notches	Lunate or crescent-shaped scars; semi-circular to arcuate shaped indentations on fracture edges with corresponding negative flake scars on medullary surfaces. Tooth notches are caused by static loading by carnivore teeth during bone fracture	Maguire et al., 1980: 83 Binford, 1981: 66 Brain, 1981: 141 Bunn, 1982: 44 Haynes, 1982: 269 Potts, 1988: 113–116 Blumenschine and Selvaggio, 1991: 30 Capaldo and Blumenschine, 1994: 725–729 Lyman, 1994: 212

* In this paper, we include these previous descriptions of damage into a single damage category, crenulated edges.
** In this paper, we include these previous descriptions of damage into a single damage category, tooth scores.

a complete juvenile red colobus monkey (*Procolobus badius*) skeleton found at Ngogo and housed at the Paleontology Museum at the University of Michigan. The entire sample is now housed at this museum under the care of W.J.S.

The original collection consists of bone fragments from 57 hunting episodes. Two kills were red duikers (*Cephalophus natalensis*), each leaving one specimen, an innominate fragment and a single tooth. These remains are not included in the analyses here to insure the smallest possible variation in damage patterns due to taxonomic, density, or structural differences. However, the damage to the red duiker innominate is similar to the damage to the red colobus innominates. In the

latter, the pelvic bone is broken and we recovered iliac blades; in the former, we recovered the part of the ilium between the acetabulum and iliac blade. The preserved fragments are similar in size, and the differences in specific parts of the ilium preserved probably relate to differences in the overall anatomy in the two taxa, as the iliac blade is more capacious in monkeys. The third sample excluded from the present analysis was the kill of a juvenile red colobus monkey which yielded only hair. The analyzed sample, then, consists of 453 bone fragments from 54 kills of 64 individuals.

Bone cleaning and bone damage identification

Most of the specimens from the 1997–2001 sub-sample (hunts 1–30, N = 262 bone fragments) were at least partially cleaned by B.L.P. with the aim of removing tissue in order to inspect bone damage more closely. Bone fragments with adhering flesh were soaked for up to a few hours in cool water. Following this, adhering tissue was removed with care taken to avoid inducing any further damage. Bones connected by soft tissue were disarticulated and re-bagged with original articulating units. We did not clean bone fragments from the 2002–2004 sub-sample (hunts 31–57, N = 192) to preserve the original condition and flesh distribution for further study. However, many specimens from this subsample have very little flesh still adhering to them. Bone damage on all of the specimens was investigated separately and then together by B.L.P. and J.D. without magnification. B.L.P. then used a 10X hand lens under high incident light to examine possible damage to all bone fragments more closely. Bone damage was identified according to previously published criteria (Table 3). We quantify and refer separately to gross bone damage (crenulated edges, peeling, fraying, step fractures, and tooth notches) and tooth marks (pits, punctures, and scores).

Results

Chimpanzee prey consumption

Teleki (1973: 141) vividly described chimpanzee prey consumption at Gombe National Park, Tanzania:

> "Small bones are thoroughly cleaned by sucking and scraping and are then chewed apart or discarded (and collected by others); large bones such as those of arms and legs are cracked between the molars, and the marrow sucked out while bones themselves are gradually consumed."

At Ngogo, chimpanzees typically process bones in the same manner. Ngogo chimpanzees often begin by disemboweling adult prey and feeding on their viscera, sometimes while the prey is still alive. They devour meat on the upper and lower long bones and chew on the articular ends of each before sucking out the marrow. Brains of adult prey are consumed last. Processing an entire carcass is time consuming; it takes several chimpanzees several hours to eat an adult monkey (Fig. 1). Chimpanzees typically share meat acquired at hunts (Mitani and Watts, 2001), and in such situations, hundreds of meters can separate small clusters of individuals who consume different parts of the same carcass.

Fig. 1. Chimpanzee at Ngogo eating the limb of a red colobus monkey.

Chimpanzee prey preference: red colobus

Chimpanzees eat a wide range of mammalian prey (Table 1). Where chimpanzees have been studied for long periods of time, however, they preferentially hunt primates, and particularly red colobus monkeys (*Procolobus badius*). Although red colobus make up 91% of the prey at Ngogo (Table 2), they do not live at especially high densities there (Mitani et al., 2000). Redtail monkeys reach densities that are three times higher than red colobus, but they form only 4% of the total prey (Table 2). Thus, chimpanzees do not prey upon red colobus in direct proportion to their population density. Recently, Stern and Goldstone (2005) found that red colobus monkeys take twice as long as other monkeys when they prepare to leap from one branch to another. This delay may allow chimpanzees to catch red colobus more easily than other arboreal primates and may account for the pattern of selective predation on them.

Ngogo assemblage: prey age and sex distribution

Chimpanzees at Ngogo take more pre-adult and female monkeys than one would expect given their proportional representations in the forest (Mitani and Watts, 1999; Watts and Mitani, 2002). These preferences are evident in the bony assemblages (Figs. 2 and 3). Pre-adult individuals, including subadults, juveniles, and infants (Struhsaker, 1975), are the vast majority of kills at Ngogo (Table 4, Fig. 2; 74% of behavioral observations of kills, 65% of bony remains of kills). This result accords with observations of the Gombe and fecal samples (Plummer and Stanford, 2000; Tappen and Wrangham, 2000). Samples from these sites consisted of 89% and 100% pre-adults, respectively. At Ngogo, the ratio of adult females to adult males in kills observed and the bone assemblage is 2.4 to 1 and 3.75 to 1, respectively. However, there is no statistical difference between the

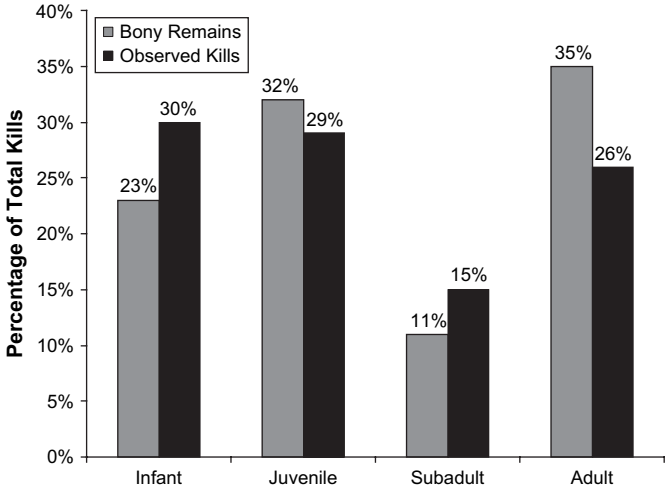

Fig. 2. Age distribution of bony remains of chimpanzee kills (this study) and observed kills (Mitani and Watts, 1999, 2001) of red colobus at Ngogo.

proportions of females to males in the observed kills and the bone assemblage ($\chi^2 = 0.76$, df = 1, $p = 0.38$).

Skeletal element representation

We analyzed 453 bone fragments of 64 individual primates from 54 observed hunting bouts (excluding the two red duiker kills). Four hundred five (89%) of these bone fragments were complete enough to be identifiable to skeletal element. Of the 49 remaining bone fragments, 9 could only be identified as long bones, and 40 could not be identified to skeletal element. Tables 5 and 6 outline the distribution of skeletal elements and anatomical regions represented in the bony assemblage.

Cranial elements dominate in terms of NISP (Numbers of Identified Specimens) followed by ribs, caudal vertebrae, and then several types of long bones (Table 5, Fig. 4). Precaudal vertebrae are conspicuously absent. This finding may be explained by previous analyses of the Gombe and fecal samples (Plummer and Stanford, 2000; Tappen and Wrangham, 2000). Vertebrae were found much more frequently in the fecal

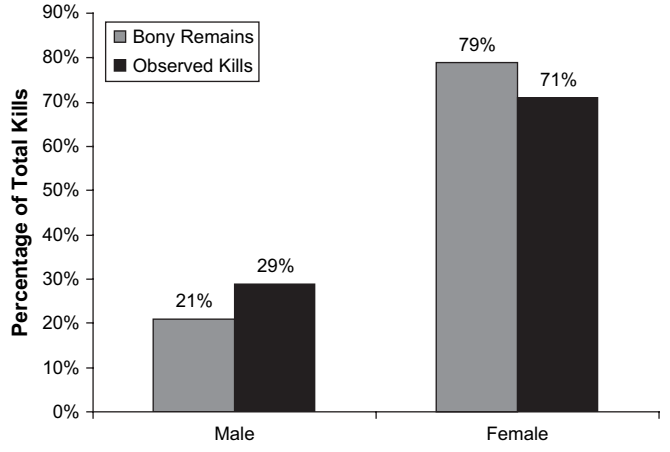

Fig. 3. Distribution of sexed males and females in bony remains of chimpanzee kills (this study) and observed kills (Mitani and Watts, 1999, 2001) of red colobus at Ngogo.

Table 4
Red colobus skeletal remains resulting from chimpanzee hunts versus observed age-sex class distribution of chimpanzee prey at Ngogo

	Skeletal samples collected					Observation	
	Females	Males	Sex not noted	Total	% of total	*Observed kills	% of total
Infant	0	0	13	13	23%	78	30%
Juvenile	0	0	18	18	32%	74	29%
Subadult	3	1	2	6	11%	38	15%
Adult	12	3	4	19	34%	68	26%
Total	15	4	37	56	100%	258	100%

* Observed kills from Watts and Mitani, 2002. Only 10 of the observed kills in Watts and Mitani (2002) were then collected and included in the skeletal sample; the remaining 46 skeletal samples were from unobserved kills. Age of infant individual was determined by observer of chimpanzee kill not by the degree of epiphyseal fusion of the long bones. Two kills, one each of juvenile and infant red colobus, yielded only hair remains with no bones; these are not included in the above chart.

sample from Kibale compared with the bony assemblage from Gombe. In these two samples, vertebrae are underrepresented both in adult and immature monkey prey, indicating that the age of prey does not contribute to this pattern. Instead, these patterns are likely a function of the relatively low bone density of vertebrae versus other primate skeletal elements (Carlson and Pickering, 2003). Additionally, these patterns could have been caused by chimpanzees chewing pre-caudal vertebrae more in order to access spinal tissue. There are no sacra or carpals present in the Ngogo sample. The only tarsals, and the vast majority of metapodials and phalanges, derive from two articulated feet: one complete foot, and one foot without the phalanges. This is consistent with the fecal sample that had a relatively high proportion of phalanges (Tappen and Wrangham, 2000). It appears that hands and feet are often eaten and digested, or possibly dropped during consumption and not recovered.

As percentages of NISP, heads (including mandibles) are the most common body part (31%), followed by hind limbs (27%), and torsos (20%). Forelimbs (13%) and hands and feet (9%) are more poorly represented (Table 6). Values of MNE (Minimum Number of Elements) are different: torso elements are most common (29%) followed closely by legs (25%), then arms (19%), heads (14%), and hands and feet (14%). Ribs make up the bulk of the axial elements, and the rest are caudal vertebrae. The dominance of legs over arms in both NISP and MNE counts may be the result of easier detachment of the arms at the shoulder joint followed by more complete consumption, especially of juvenile prey.

Crania are the most fragmented elements; this results in a dominance of cranial bones in terms of NISP, but not MNE (Table 5, Fig. 4). The average and range of cranial fragmentation (NISP/MNE) are not strongly affected by prey age (Table 7). Following the cranium, the scapula, mandible, and innominate are the next most fragmented elements, in that order.

Calculations of bone survivorship underscore the relatively high representation of skulls, especially crania (57%), followed by hind limb elements, then forelimb elements, as well as the absence of vertebrae, except caudals (Tables 5

Table 5
Red colobus prey skeletal elements: number of identified specimens (NISP), minimum number of elements (MNE), bone survivorship, and bone fragmentation (NISP/MNE)

Skeletal element	NISP	% of total NISP	Observed MNE	% of total MNE	Expected MNE	% MNE survivorship	Fragmentation (NISP/MNE)
Cranium	126	31%	33	1%	58	57%	3.82
Mandible	13	3%	9	3%	58	16%	1.44
Clavicle	2	<1%	2	1%	116	2%	1.00
Scapula	9	2%	6	2%	116	5%	1.50
Humerus	19	5%	17	6%	116	15%	1.12
Radius	14	4%	14	5%	116	12%	1.00
Ulna	13	3%	13	4%	116	11%	1.00
Pelvis	16	4%	13	4%	58	22%	1.23
Sacrum	0	n/a	0	n/a	58	n/a	n/a
Femur	27	7%	27	9%	116	23%	1.00
Tibia	25	6%	25	8%	116	22%	1.00
Fibula	13	3%	13	4%	116	11%	1.00
Carpals	0	n/a	0	n/a	464	n/a	n/a
Tarsals	13	3%	13	4%	406	3%	1.00
Metapodials	10	2%	10	3%	290	3%	1.00
Phalanges	18	4%	18	6%	870	2%	1.00
Ribs	59	15%	59	20%	1392	4%	1.00
Cervical	0	n/a	0	n/a	406	n/a	n/a
Thoracic	0	n/a	0	n/a	696	n/a	n/a
Lumbar	0	n/a	0	n/a	406	n/a	n/a
Caudal	28	7%	28	9%	1508	2%	1.00
Total	405		300		7598	4%	

Percentage of total NISP and MNE were calculated by dividing the NISP or MNE of a particular skeletal element by the total NISP (405) or MNE (300) of the entire sample. Percentage MNE survivorship was calculated by dividing the observed MNE value of a particular skeletal element by its expected MNE value. The expected value is the number of times a particular skeletal element occurred in the 58 red colobus individuals in the sample including the 2 kills mentioned above from which no remains were recovered. See Brain (1981) and Pickering (2001a) for use of this technique. Expected values for caudal vertebrae are derived from Schultz (1961). Unidentifiable bones were excluded.

and 6, Fig. 5). Though ribs contribute disproportionately to the overall NISP and MNE, they still have low survivorship. This is consistent with the Gombe sample where crania have the highest survivorship (60%) and axial postcranial elements have the lowest survivorship (17–20%) (Plummer and Stanford, 2000). However, in contrast to the Gombe sample, we did not find mandibles or scapulae to have a particularly high survivorship; the reason for this discrepancy is unclear. Mandible survivorship was 40% at Gombe and 16% at Ngogo, and scapula survivorship was 30% at Gombe and 5% at Ngogo.

Bone damage

The low overall proportion of tooth marking (4.4% of NISP) is consistent across the two sub-samples: the fully cleaned bone fragments ($n = 9$ tooth marked out of 262, 3.4%) and uncleaned bone fragments ($n = 11$ tooth marked out of 192, 5.7%). Tooth marked specimens refer only to bones with tooth pits, punctures, or scores; other types of damage are analyzed separately. Table 3 outlines the criteria we used to identify tooth marks as well as other types of bone damage, and Table 8 lists the tooth marked bone fragments from the Ngogo chimpanzee kill sample. It is worth noting for comparative purposes that we found only one tooth notch, on a subadult red colobus tibia.

Table 6
Distribution of anatomical regions represented in the red colobus prey assemblage

Anatomical region	NISP	% total NISP	MNE	% total MNE	% MNE survivorship
Head (cranium, mandible)	139	31%	42	14%	36%
Torso (including tail)	87	20%	87	29%	3%
Arm (with scapula and clavicle)	57	13%	55	19%	9%
Leg (with innominate)	121	27%	73	25%	13%
Hands and feet	41	9%	41	14%	2%

Crania. Crania, especially cranial vaults, are highly fragmented resulting in many isolated pieces. All parts of the cranium are present, but no single intact cranium is present. This fragmentation probably occurred when the chimpanzees were attempting to access the brain. Isolated maxillae are fairly common, but no isolated primate teeth were recovered. Cranial fragments are broken both between bones (along sutures) and within individual cranial bones. The only three mainly intact splanchnocrania (faces) are from adult prey (Fig. 6a). On these specimens, all crania (especially orbits) are damaged even more extensively than in crowned hawk-eagle kill samples from Ngogo and the Tai forest in West Africa (Sanders et al., 2003; McGraw et al., 2006).

Only 4 of the 126 cranial fragments exhibit chewing damage (2 cleaned, 2 not cleaned). However, 27 specimens (21%) have incipient fractures where fracture lines, likely from fragmentation, perpetuate incompletely through the bone (Fig. 6b). This type of damage was described as compression cracking

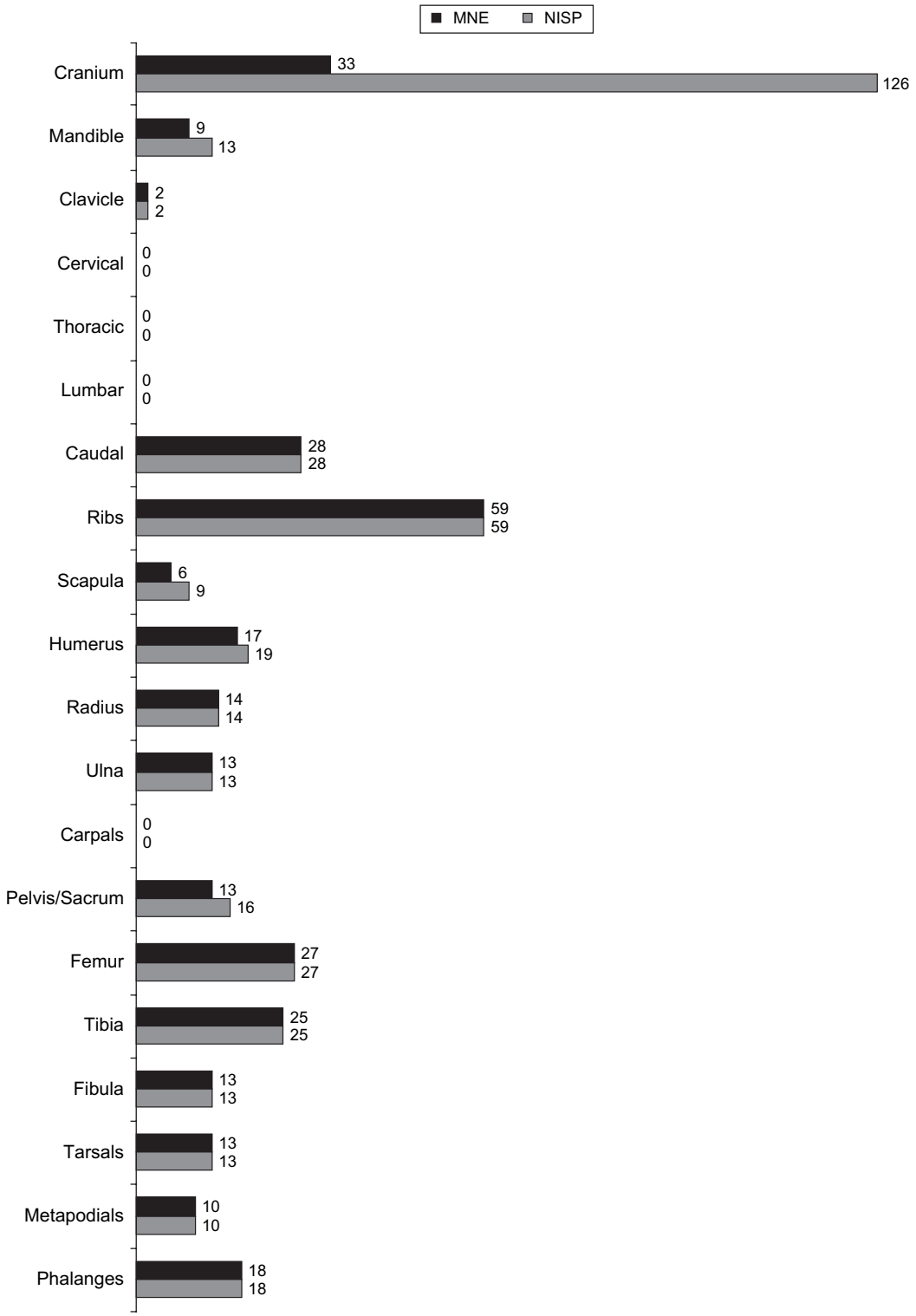

Fig. 4. Skeletal element abundance (MNE: black; NISP: grey) of bony remains from primate kills at Ngogo studied in this analysis.

and was observed on a single young juvenile cercopithecine eaten by a crowned hawk-eagle (Sanders et al., 2003: 98). Older juveniles and sub-adults in the eagle sample did not suffer damage to their crania in the same way, but several cranial remains show obvious signs of having been deformed by pressure. Compression cracking is also observed in the Gombe assemblage (Plummer and Stanford, 2000: 358). Compression cracking is found on both adult and pre-adult monkey specimens from Ngogo, and may be indicative of, though certainly not exclusive to, monkey bones modified by chimpanzees.

A single adult red colobus monkey cranial specimen has a tooth puncture in the thin zygomatic bone posterior to the zygomatic arch (Fig. 6c). The other tooth punctures in the cranial sample are on an infant chimpanzee that was killed and

Table 7
Fragmentation of primate crania by age class

Age class	N	Cranial NISP	
		Average	Range
Infant	12	3.1	1–10
Juvenile	2	3.5	3–4
Subadult	5	4.6	1–12
Adult	12	3.7	1–10

N = Number of individuals in that age class that had any cranial remains. The average cranial NISP was calculated by summing the total number of cranial specimens from all individuals in that age class and dividing by the number of individuals in that age class. Two kill samples contained remains of two individuals with indistinguishable cranial elements, a juvenile and an infant; these are not included.

cannibalized, rather than hunted, as are monkey prey. This specimen has three tooth punctures: one in the occipital, one behind the right supraorbital rim, and one above the right supraorbital. The total tooth-marked cranial NISP and MNE are 1.6% and 6.1%, respectively. All tooth marks on crania are tooth punctures.

Mandibles. Mandibular breakage by Ngogo chimpanzees generally resembles chewing damage by larger carnivores on medium to large prey and by smaller carnivores on small prey (Fig. 7; Blumenschine, 1986; Andrews, 1990: 56, mandible damage category C). Mandibular condyles are often missing, and coronoid processes, the attachment sites for the temporalis muscles, are either entirely destroyed or damaged. The lingual and inferior surfaces of several mandibular specimens have damage consistent with the muscles of the floor of the mouth (anterior digastric, mylohyoid, and the geniohyoid; Swindler and Wood, 1982) being pulled away from the bone. This damage pattern is consistent with consumption of the tongue. On two of the mandibles, the inferior aspect of the horizontal ramus is completely chewed off, presumably to access the marrow under the cheek teeth. Three of the 13 mandibles (23%) exhibit tooth marks (Table 8): one has a score on the lateral side of the left horizontal ramus; one has two pits on the medial side of the horizontal ramus; and one has three punctures on the left horizontal ramus (one on the medial side and two on the lateral side).

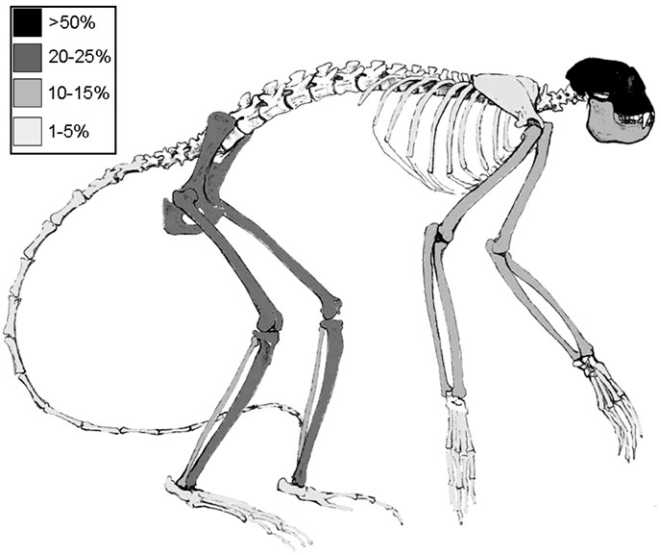

Fig. 5. Percentage MNE survivorship of primate kills at Ngogo. See Table 5 for details on how percentage MNE survivorship was calculated. Skeleton outline from Kingdon (1974: 168), drawing of a black and white colobus monkey skeleton.

Clavicles. The two clavicles in the Ngogo sample are from two different adult red colobus monkeys. The cleaned clavicle exhibits chewing damage on both ends (one end is crenulated and the other frayed); the other clavicle that is not cleaned is undamaged.

Ribs. Ribs are generally nearly complete with damage concentrated on one or both ends. Out of 59 ribs, only 19 (32%) do not exhibit any damage; 13 of those 19 ribs are not cleaned. Sixteen rib ends are frayed, one is peeled, one is step-fractured, and 21 are crenulated. Both caudal and cranial ends are damaged. Fourteen specimens (24%) exhibit transverse incipient breaks. This may result from the chimpanzees swinging the monkeys around and hitting them on trees or other objects while killing them, especially younger prey (J.C.M., pers. observ.; Fig. 8). Surprisingly, there are no tooth marks found on any ribs; it might be expected that removing the relatively thin overlying muscle bodies from the rib cage would have caused tooth marks.

Vertebrae. The only vertebrae present in the assemblage are caudal (tail) vertebrae. Twenty-one of the 28 caudal vertebrae (75%) come from two individual prey animals. These bones are still articulated to each other and fleshed, making damage on these specimens impossible to see. Of the remaining seven isolated and cleaned specimens, six (86%) have longitudinal fractures. None of these seven vertebrae examined exhibit tooth marks.

Scapulae. Regardless of whether the scapulae are cleaned ($n = 7$) or not ($n = 2$), they are damaged in a consistent manner: the glenoid is missing, possibly consumed while accessing the arm, with either incipient fractures and/or crenulated edges present around the margin of the scapular blade (Fig. 9). Similar damage is illustrated in a figure but not described by Plummer and Stanford for the Gombe sample (2000: 357). The scapulae do not exhibit any tooth marks.

Innominates. The innominates exhibit distinctive damage. Every one of the 16 innominates (5 cleaned, 10 not cleaned) is reduced to its iliac blade (Fig. 10). Presumably, the pubes and ischia were consumed while the chimpanzees were accessing the monkeys' pelvic organs and abdominal tissues. Six of 16 ilia (37.5%) exhibit crenulated edges or fraying on the posterior, superior, and lateral edges where the gluteus medius muscles originate. Also, the superior aspect of the acetabulum, where femoris and gluteus minimus muscles originate in cercopithecoids, is often frayed. Some of this damage may have occurred while lower limbs were being disarticulated from the rest of the carcass. Four of the 16 (25%) ilia are tooth marked (one cleaned, three not cleaned). The five tooth marks on these ilia, including one puncture, one pit, and three scores, are located on or near the auricular surface on the medial side of the iliac blade (Table 8).

Long bones. As reported in other studies (Pickering and Wallis, 1997; Plummer and Stanford, 2000), long bones chewed by chimpanzees at Ngogo exhibit distinctive damage

Table 8
Tooth marked bones from chimpanzee kills at Ngogo

Skeletal element	Prey (kill number)	Type and location of tooth mark(s)
Cranium (face)	Adult female red colobus (#10)	Tooth puncture on thin bone (lateral)
Cranium (top)	Infant chimpanzee (#57)	Three tooth punctures: one in the occipital, one behind the right supraorbital rim, and one above the right supraorbital
Mandible	Adult female red colobus (#1)	Tooth score on lateral side of left horizontal ramus
Mandible	Adult female redtail (#3)	Two pits on medial side of the horizontal ramus
Mandible	Adult male black and white colobus (#4)	Three punctures on left horizontal ramus (one medial, two lateral)
Innominate	Adult female red colobus (#31c)	Tooth score, near margin
Innominate	Juvenile red colobus (#11)	Tooth pit on iliac tuberosity, anterior
Innominate	Subadult female red colobus (#51)	Tooth score, lateral
Innominate	Subadult female red colobus (#51)	Two tooth scores, lateral
Femur	Adult male red colobus (#42)	Three tooth scores, shaft
Femur	Juvenile red colobus (#34)	Tooth score, shaft
Femur	Subadult female red colobus (#33)	Three tooth scores, all associated with chewed metaphysis end
Humerus	Adult female red colobus (#10)	Two tooth pits on humeral head
Humerus	Infant red colobus (#5)	Tooth score near chewed metaphysis end
Humerus	Infant red colobus (#18)	Tooth score, shaft
Radius	Adult female red colobus (#2)	Tooth pit, associated with chewed metaphysis end
Fibula	Adult female redtail (#49)	Two tooth scores, one shaft, one near chewed metaphysis end
Long bone	Adult male red colobus (#32)	Tooth score near frayed edge
Non-identifiable bone	Adult male red colobus (#55)	Two scores in association near broken edge of bone

patterns. At least one end of nearly all long bone specimens from Ngogo is destroyed (117 out of 120; 98%), leaving characteristic fraying, step fracturing, and crenulation on the ends of the remaining diaphyses (Fig. 11). The Ngogo sample has a higher frequency of missing limb ends (98%) than the Gombe sample where 62.5% of the long bone ends were chewed off (Plummer and Stanford, 2000). This damage pattern seems to result from chimpanzees chewing off the greasy, less-dense limb ends in order to suck out the marrow from the long bone shafts (J.C.M., pers. observ.).

Nearly half of the total sample of tooth marked specimens from Ngogo (9 out of 20; 45%), defined as a specimen with at least one tooth mark present, are long bones (four cleaned, five not cleaned; Table 8). These include three femora (not cleaned, with seven scores); three humeri (all cleaned, with three pits and two scores); one radius (cleaned, with one pit); one fibula (not cleaned, with two scores); and one long bone (cleaned, with one score).

We can relate long bone damage patterns, particularly on the tibiae, to removal of particular muscles during consumption. On the majority of the tibiae present in the assemblage, the proximolateral side of the bone was broken away, but the proximomedial side was still present and usually bent posteriorly (Fig. 12). The lateral side of the proximal end of the tibia is where the tibialis anterior, fibularis longus, and extensor digitorum longus muscles originate. Damage on the medial side may be a product of the chimpanzee pulling on the semimembranosus or popliteus muscles that insert on the medial side, and would result in a posterior bending of the bone if the muscles were torn from their origins.

Tarsals, metapodials, and phalanges. All of the tarsals and nearly all of the metapodials and phalanges in this sample derive from two articulated feet of adult red colobus that still have some fascia covering the bones. The single metapodial from a different individual is crenulated on the ends, and one of the metapodials from the foot missing the phalanges has a small amount of bone missing on the distal end. Besides the articulated feet, there are three phalanges from two different juvenile red colobus individuals. Two of these from one individual, an intermediate and distal phalanx, exhibit longitudinal fracturing and fraying, respectively. The third, a distal phalanx from a different individual, has no damage. None of the tarsals, metapodials, or phalanges exhibit tooth marks.

The fecal sample also had a low proportion of modified or gastrically corroded hand and foot elements (17%; Tappen and Wrangham, 2000). Interestingly, there is also an absence of corrosive damage from digestion on baboon hand and foot bones fed to leopards and hyenas (Pickering, 2001b), but the mechanisms accounting for the lack of damage on hand and food bones in the Ngogo sample versus the carnivore and fecal samples are different. In the Ngogo sample, the low damage on these elements is probably due to chimpanzees dropping or abandoning these parts, while in carnivore scat, it is probably because the skin acted as a protective barrier during ingestion (Tappen and Wrangham, 2000; Pickering, 2001a,b).

Discussion

The Ngogo sample exhibits specific taphonomic patterns that we contend are characteristic of a chimpanzee-modified prey assemblage. These patterns include low taxonomic diversity (in this case, with a predominance of red colobus monkeys) and an age distribution skewed towards pre-adults. The skeletal remains are dominated by cranial bones, followed by long bones,

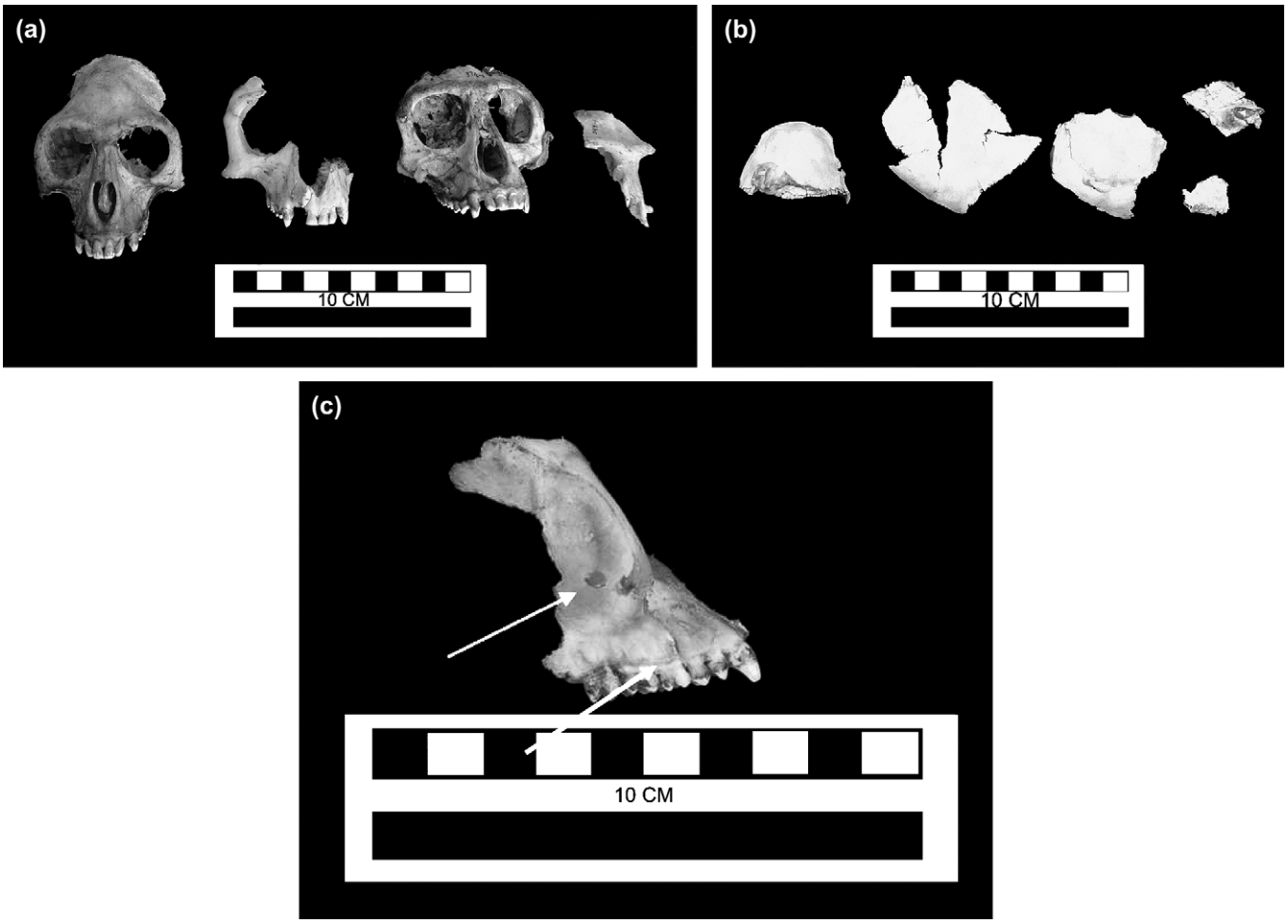

Fig. 6. (a) All of the relatively intact red colobus cranial (face) specimens from the Ngogo assemblage. (b) The entire sample of cranial remains from a single adult red colobus from the Ngogo assemblage. Note conspicuous compression fracturing on the second specimen from the left. (c) Maxilla of an adult female red colobus with two tooth punctures indicated by the arrows.

and ribs. Pre-caudal vertebrae are absent. Long bone epiphyses are usually chewed off, leaving fraying, peeling, and crenulated edges on the diaphyseal ends. Cranial bones are highly fragmented and often exhibit compression cracking, and innominates are destroyed except for iliac blades. Tooth marks are uncommon (4.4% of total NISP; 3.4% of cleaned bone fragments, 5.7% of uncleaned bone fragments).

The comparative approach

Three factors make it difficult to compare frequencies of particular types of bone modification among studies of chimpanzee taphonomy. First, some publications did not describe particular categories of bone damage. For example, Tappen and Wrangham (2000) do not report peeling, but did report

Fig. 7. A series of mandibles from the Ngogo sample. Note the destruction of most of the vertical rami (white arrows) and the damage to some of the inferior aspects of the horizontal rami (grey arrow), both leaving crenulated edges.

Fig. 8. A series of ribs from the Ngogo sample. Note the transverse incipient fractures on all of the specimens indicated by the white arrows.

fraying; the opposite is the case for Pickering and Wallis (1997) and Plummer and Stanford (2000). Whether this is because these types of damage were not present in the Gombe assemblage, or because the researchers called them something else, is unclear. Pickering and Wallis reported all damage they observed in the captive assemblage (Pickering, pers. comm.), and this is presumed for the other studies. Second, previous studies did not consistently state whether a bone fragment could exhibit more than one damage category (e.g., Pickering and Wallis, 1997, Table 2), making cross-assemblage patterns of overall damage frequencies, defined by NISP with damage, problematic.

Third, for the purpose of establishing a recognizable taphonomic signal of chimpanzee consumption of small prey, it is necessary to compare damage patterns from the Ngogo assemblage to that of other predators on *similar sized prey*. These predators include small carnivores (Andrews and Nesbit-Evans, 1983; Andrews, 1990; Elkin and Mondini, 2001),

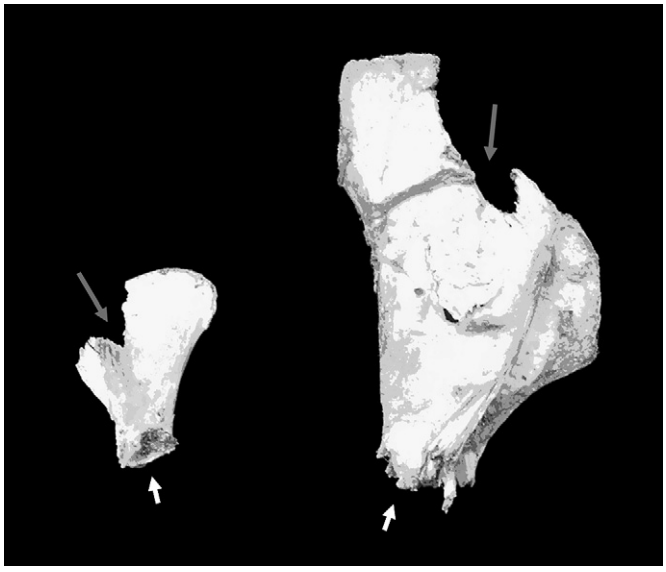

Fig. 9. Scapulae from the Ngogo sample (left from a juvenile, right from an adult). Note the absence of the glenoids (white arrows) and chewing damage resulting in crenulated edges (grey arrows) on the scapular blades.

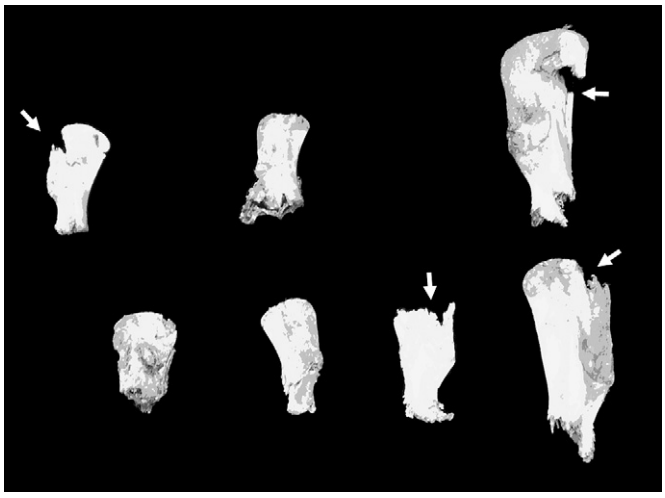

Fig. 10. A series of innominates from the Ngogo sample. Note the consistent damage and how ilia are the only bones present. Also note the chewing damage leaving crenulated edges around the superior margins of some of the ilia (white arrows).

leopards (Simons, 1966; Brain, 1981; de Ruiter and Berger, 2000; Pickering and Carlson, 2002; Carlson and Pickering, 2003, 2004), black and crowned hawk-eagles (Brain, 1981; Berger and Clarke, 1995; Sanders et al., 2003; McGraw et al., 2006), and humans (Binford 1978, 1981; Maguire et al., 1980; Brain, 1981; Gifford-Gonzalez, 1989; Oliver, 1993; Elkin and Mondini, 2001; Landt, 2004). Comparing general skeletal element patterns or tooth mark frequencies among prey assemblages of very disparate sizes is inappropriate because mammalian predators normally have specific prey size ranges. Even if overall skeletal element profiles and damage patterns are similar, the prey size ranges from which the skeletal element profiles are generated are not. For example, it is uninformative to compare bone damage patterns of lions and hyenas to that of chimpanzees with the aim of identifying unique taphonomic aspects of each predator. Lions and hyenas almost always completely consume prey the size of red colobus monkeys (B.P., pers. observ.). For these reasons, we compare the damage on primates inflicted by chimpanzees to damage on similar sized prey inflicted by leopards, hawk-eagles, and humans.

Skeletal element frequencies. Skeletal element frequency data are useful for cross-assemblage comparisons. Naturally, though, there may be taphonomic factors that affect assemblages in different ways. For instance, while skeletal element profiles of leopards feeding on baboons are conditioned by intrinsic properties of bones, such as bulk mineral density and volume, there is a bone size threshold beneath which density contributes little to mediating predator damage to and destruction of skeletal elements (Carlson and Pickering, 2003). We think that skeletal element frequency comparisons are most useful between assemblages that 1) include full versus partial carcasses in order to maximize skeletal element profile comparability; 2) are based on the same type of collection (e.g., scats, dens) in order to minimize possible differences based on collection type versus predator identity; and 3) report systematic

Fig. 11. A series of limb bones from Ngogo with the characteristic damage pattern of chewed off epiphyses and damaged (frayed – white arrows, peeled – white triangles, and crenulated – grey arrows) limb bone cylinder ends.

NISP or MNE data, or derivations of these counts, making direct comparisons possible.

For the Ngogo sample, given the above recommendations, the only possible comparisons are with 1) baboon bones found in leopard-inhabited caves in Kenya (Simons, 1966), and 2) a ''refuse'' assemblage derived from 10 baboons fed to captive leopards (Pickering, 2001a). In both instances, the prey bones are from a single species of primate, eliminating potential bias due to differences between prey species. Additionally, similar kinds of data are available for the assemblages including each skeletal element's percentage of the total NISP (Simons, 1966; Fig. 13) and percentage of MNE survivorship (Pickering, 2001a; Fig. 14). However, if any dismemberment of the baboons occurred prior to their carcasses reaching the caves, skeletal element frequency would have been altered by transport rather than consumption, making this a more problematic comparison. Also, the assemblage from the caves in Kenya is likely a palimpsest with multiple unrelated samples that accumulated over a significant time interval.

Many similarities exist between these chimpanzee- and leopard-modified primate assemblages including: 1) a predominance of cranial remains; 2) higher representation of hind limb versus forelimb elements; 3) more upper (femur, humerus) versus intermediate (tibia, fibula, radius, ulna) limb bones. The leopard cave and Ngogo chimpanzee kill assemblages are especially similar in the absence or low preservation of carpals and poor preservation of pre-caudal vertebrae, and the rank orders of the proportions that each skeletal element contributes to the total NISP in the two samples are similar ($Rs = 0.6110$, $p = 0.0025$; Fig. 13). However, the relatively high representation of ribs in the Ngogo sample differs from the leopard cave sample. The rank orders of percentage MNE survivorship of skeletal elements from the Ngogo sample and the refuse assemblage are also similar ($Rs = 0.8023$, $p < 0.0001$; Fig. 14).

Bone damage patterns. Several authors have cautioned against the automatic attribution of all mastication damage at early archaeological sites to carnivores, and have suggested that there could be convergence of hominin and carnivore chewing damage patterns (e.g., Pickering and Wallis, 1997; White, 1992). While we agree that further investigation of bone damage patterns by different taphonomic agents to identify unique taphonomic ''signatures'' of involvement by different predators is useful and commendable, we cannot overemphasize the necessity of considering prey size in taphonomic analyses. While the overall ''patterns'' of bone damage (e.g., skeletal element profiles and intra- and inter-bone damage patterns such as a preponderance of limb shafts versus limb ends) by chimpanzees, eagles, some smaller carnivores, and humans may be similar, most larger carnivores that have been implicated in the formation of archaeological sites, especially spotted hyenas, possess completely different bone destruction capabilities than other predators. Therefore, we fully agree with Pickering and Wallis (1997) that a contextual or configuration approach must be taken when analyzing bone damage patterns to include variables such as site setting, prey species, and prey size. To this end, we also stress the utility of naturalistic observations of predator bone modification

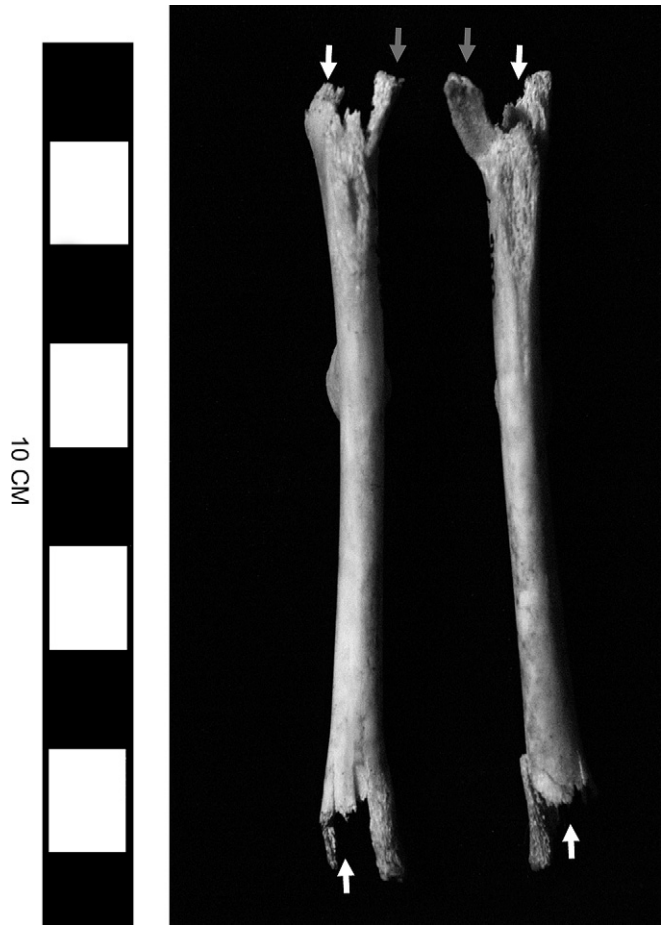

Fig. 12. The two tibiae from an adult red colobus from the Ngogo sample, anterior view. Note the consistent damage including the missing epiphyses and fraying (white arrows) and the pulling outwards of the proximomedial limb ends (grey arrows).

whenever possible over experiments employing artificial prey samples that predators are not expected to encounter naturally.

1. Small carnivore bone damage. In an experiment feeding sheep bones to Pampa or Azara's red foxes, Elkin and Mondini (2001) found tooth marks on 3 of 12 ribs (25%), 2 of 3 scapulae (66%), 2 of 3 humeri (66%), 2 of 3 ulnae (66%), 1 of 3 radii (33%), 2 of 6 carpals (33%), and none of the vertebrae. The total tooth marked NISP is 12 out of 30 (40%), much higher than the tooth-marked NISP at Ngogo (4.4%).

2. Leopard bone damage. Simons (1966) noted leopard chewing damage on various parts of baboon crania from caves in Kenya including the lateral pterygoid plates (68%), zygomatic arches (54%), and supraorbital rims (36%). He also noted tooth marks in the outer borders (63%) and inner walls (45%) of the orbits and on one or both sides of the rostrum (54%). He also observed a number of skulls with small tooth pits on the occipitals, parietals, and temporals. The high proportion of damage by leopards on baboon crania relative to other skeletal elements is similar to that of chimpanzees that inflict significant amounts of damage on colobus monkey crania, though leopards inflict even higher damage frequencies to crania (up to 68% for leopards versus 24% for chimpanzees, including incipient fractures). Simons (1966) noted that only one juvenile baboon brain was accessed indicating an inability of the leopard to fragment adult baboon crania. Simons (1966) mentioned that 13 of the 14 mandibles examined had one or both of their ascending rami chewed off, similar to the Ngogo assemblage, but with a higher proportion of damage on mandibles in the leopard sample. He observed chewing damage on "several" baboon vertebrae, noted that scapular blades were "usually" chewed, and noted that the ends of the limb bones were "usually" chewed off. In Simons' (1966) sample, 21 of 32 (66%) proximal femora, 20 of 32 (63%) distal femora, 7 of 8 (88%) proximal tibiae, and 5 of 8 (63%) distal tibia ends were missing. He did not note any damage on the few hand and foot bones recovered. Brain (1981: 296–297) also listed skeletal elements present for four leopard lair assemblages, and noted damage to some, but did not describe this damage in detail.

Leopard damage to baboons shares many similarities to chimpanzee damage to red colobus monkeys. However, the size difference between larger baboons (11–50 kg, Kingdon, 1974) and smaller red colobus monkeys (7.5–12.5 kg, Kingdon, 1974) suggests that characterizing leopard damage to smaller primate prey would be an even more useful comparison.

3. Eagle bone damage. The remains of hyraxes, the preferred prey of black eagles in more open country or rocky settings, include mainly cranial parts, innominates, and a few limb bones (Brain, 1981). Their crania exhibit characteristic damage where the braincases are opened from the back or side by the eagles' beaks to remove the brain. This pattern is unique to these birds of prey and not seen in the Ngogo chimpanzee kill sample. Damage to hyrax mandibles by black eagles is also common. Berger and Clarke (1995) observed similar damage by black eagles to vervet monkey skulls as Brain (1981) saw on hyraxes, and their description of damage by black eagles to vervets is largely consistent with Brain's (1981) descriptions of damage to hyraxes.

Sanders et al. (2003) recorded very low frequencies of bone damage by crowned-hawk eagles to cercopithecoid prey at Ngogo (<50% for nearly all skeletal elements of all prey species; cf. McGraw et al., 2006, in the Tai forest sample). At Ngogo, most adult crania were intact but damaged and accompanied by mandibles, though maxillae were sometimes missing (Sanders et al., 2003). Adult monkey crania in the Ngogo eagle kill sample, which have the highest bone survivability of all of the skeletal elements (especially in pre-adult individuals), show only subtle signs of damage with few notable marks except for punctures around the orbits and breakage to access the brain. An independently collected prey sample from the Tai forest had signs of slightly more aggressive manipulation from eagle talons and beaks (McGraw et al., 2006), but this is still minimal compared with the chimpanzee-damaged sample from Ngogo.

Signs of eagle manipulation at Ngogo and Tai included punctures, talon nicks, and "can-opener" perforations. The latter two are apparently unique to eagle-modified prey (Brown, 1971; Andrews, 1990; McGraw et al., 2006; Trapani et al., 2006). At Ngogo, eagles tore open juvenile and infant

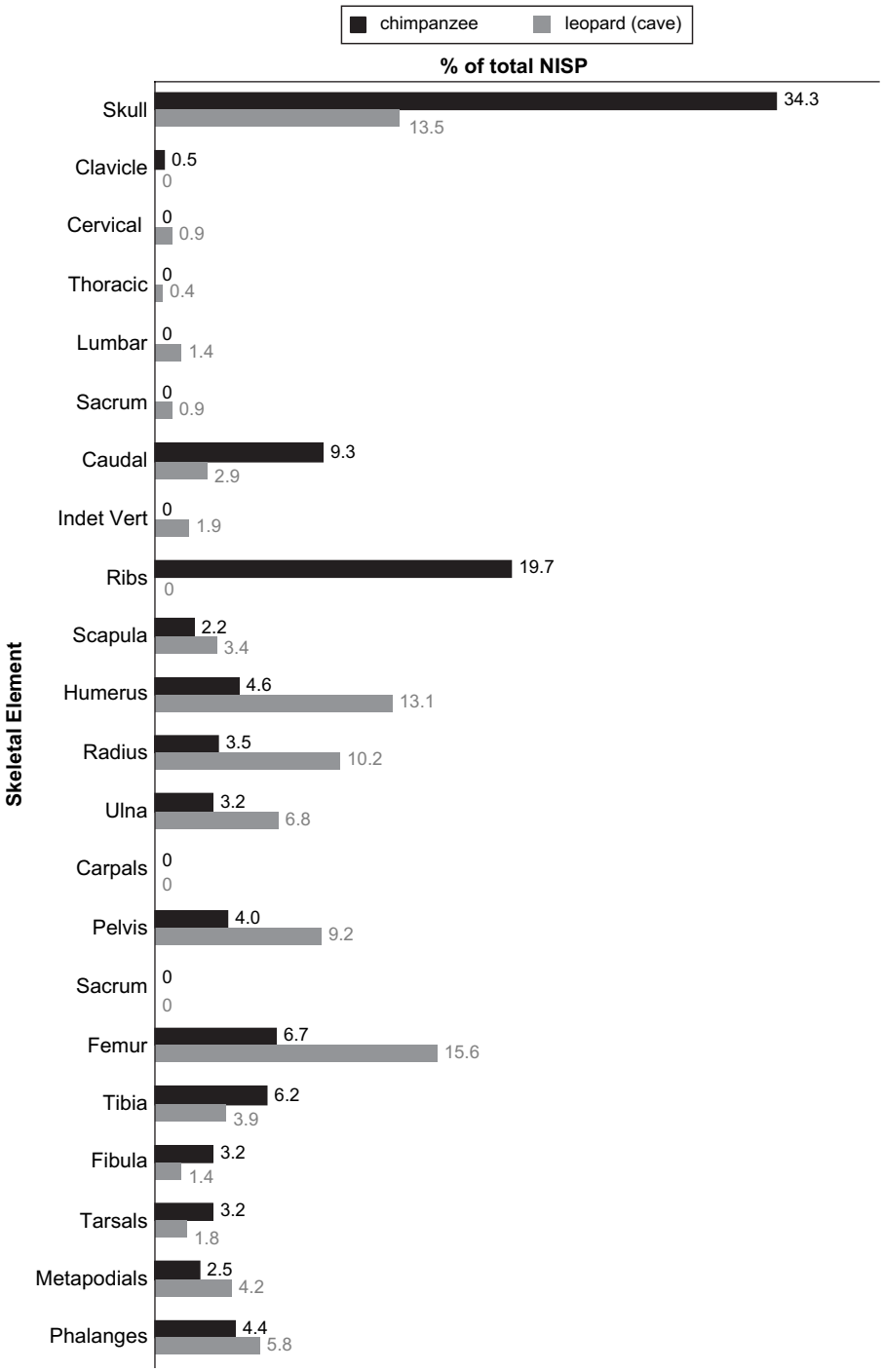

Fig. 13. Comparison of skeletal element NISP data between red colobus monkeys from Ngogo and baboons from leopard cave assemblages. Leopard cave assemblage data from Simons (1966). Percent of total NISP is the contribution each skeletal element makes to the total NISP. Skull refers to both crania and mandibles. Percentages were rounded to the nearest tenth of a percent.

splanchnocrania, one of which showed compression cracking similar to that seen in the Ngogo chimpanzee-modified assemblage (Sanders et al., 2003; Trapani et al., 2006). Mandibles at Ngogo were commonly left undamaged (78%), and the two mandibles that were damaged each had only one modified ramus (Sanders et al., 2003). At Tai, nearly all mandibles were undamaged (McGraw et al., 2006). In contrast, nearly all scapulae from assemblages at Ngogo and Tai had a unique damage pattern of shattering and raking (Sanders et al., 2003; McGraw et al., 2006) not seen in the Ngogo chimpanzee kill assemblage, but observed in other predatory bird assemblages (Andrews, 1990).

Long bones at Ngogo are mostly undamaged by eagles, and a few are minimally damaged on their articular ends (32 to 46% and 24 to 34% in forelimbs and hind limbs, respectively). This is very different from the Ngogo chimpanzee kill

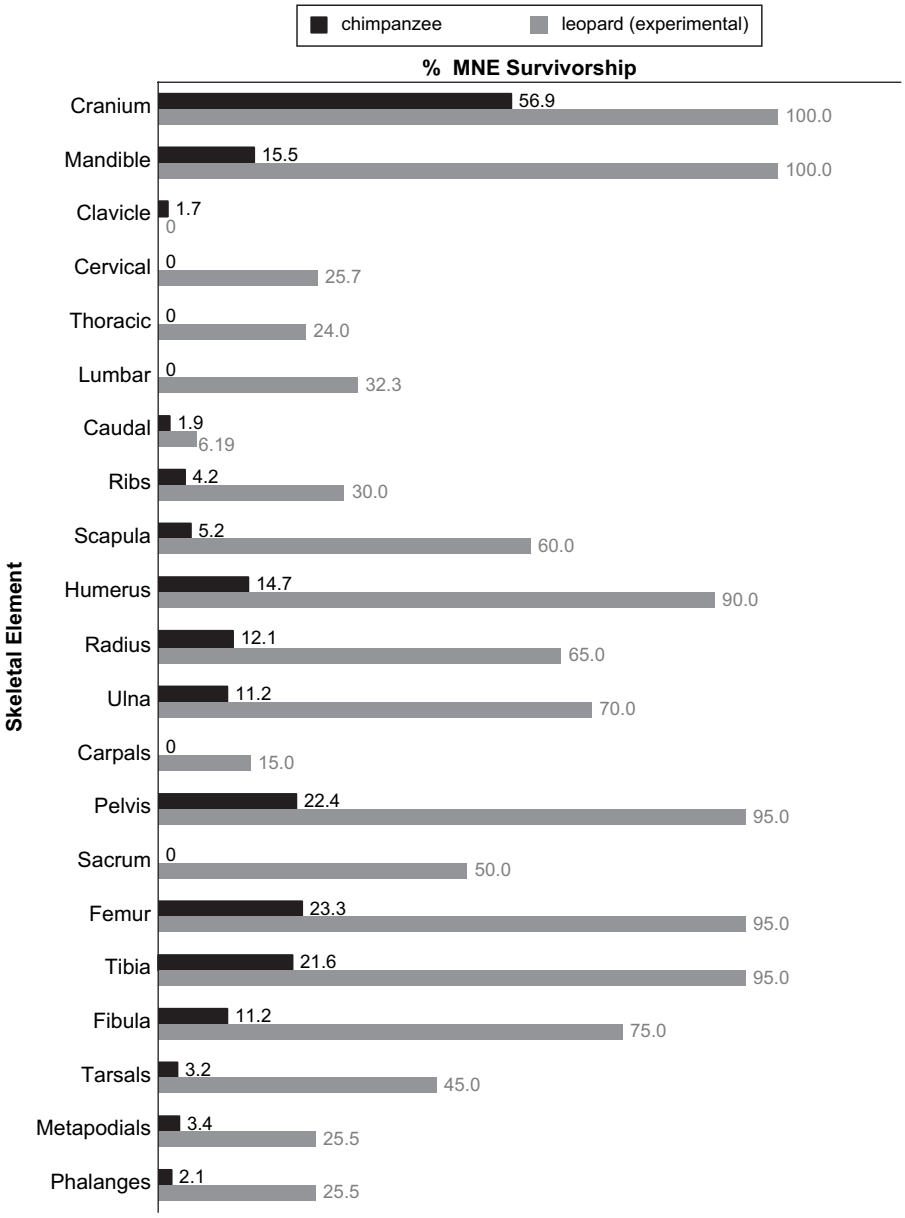

Fig. 14. Comparison of skeletal element % MNE survivorship data between red colobus monkeys from Ngogo and an experimental leopard feeding refuse assemblage of baboons. Baboon assemblage data from Pickering (2001a). See Table 5 for details on how % MNE survivorship was calculated. Metapodial % MNE survivorship is an average of metacarpal and metatarsal, and phalanges % MNE survivorship is an average of 1st, 2nd, and 3rd phalanges. Percentages were rounded to the nearest tenth of a percent.

assemblage where 98% of limb articular ends are chewed off. Also, there are occasionally midshaft fractures on forelimbs (17–23%) and hind limbs (11–16%) in the eagle sample. This is not observed in the chimpanzee kill assemblage from Ngogo, nor is the unique damage described above to crania and scapulae.

4. Human bone damage. Modern human damage to the skeletal remains of small prey has not been investigated as systematically as in carnivores, but there are several relevant studies. We do not here consider human and chimpanzee experimental gnawing damage to bird bones (e.g., Weisler and Gargett, 1993; Landt, 2004) because of structural differences in mammalian versus avian bones. In addition, many of the human groups studied used metal knives and sometimes boiled the small mammals they ate to extract the marrow and grease (e.g., Oliver, 1993; Landt, 2004; Nicholson, 2005). This changes how they process these prey animals and renders strict, quantitative comparisons of bone damage patterns inappropriate. For instance, in only 39% of the marrow-bearing long bones in Landt's (2004) small mammal sample (which included blue duikers, brush-tailed porcupines, giant pouched rats, and murid rats and mice) was access to marrow attained, and very few long bone cylinders were present. This proportion is much lower than in the Ngogo chimpanzee kill assemblage where 98% of long bones had missing ends indicative of marrow exploitation. This difference is probably because

metal knife technology precludes the removal of edible tissue using only hands and teeth, the latter likely causing higher levels of bone damage.

Still, descriptive accounts of human gnawing damage on cooked bones are useful to determine what humans *can* do to small mammal bones. Binford (1978, 1981) observed Nunamiut chewing the margins of vertebrae, ribs, innominates, and scapulae, which sometimes resulted in mashed edges and pitting. He also observed the Nunamiut fairly commonly gnawing on short rib sections during fresh meat consumption. He noted human gnaw marks on spinous processes of thoracic vertebrae and proximal margins of scapulae on "soft" bones of immature individuals. He found punctures to be rare and scoring absent but noted crenulated edges and step fractures. Gifford-Gonzalez (1989) noted bone damage to 10 caprine limb bones consumed and discarded by Kenyan pastoralists with one tooth score (0.5%, N = 2010 identifiable bones). Rather than a particular pattern of damage or observed consumption, Gifford-Gonzalez (1989) attributes the damage on these bone specimens, nine of which were bone cylinders, to humans based on 1) lack of evidence for carnivore consumption, and 2) bones with similar damage in her sample of human butchered and consumed bones. She does not describe the human chewing damage, but notes that it is always on the ends of the bone cylinders. Brain (1981) noted that Khoikhoi people gnawed and swallowed goat caudal vertebrae and severely damaged the ends of limb bones such as femora and metapodials. Maguire et al. (1980) found ragged-edged chewing damage (similar to that caused by hyenas) on goat bones eaten by Khoikhoi, especially on scapulae and pelves. They also noted crushing damage by human teeth on some of the goat bones. Elkin and Mondini (2001) found human tooth marks on 48% of bones from a "barbecue" feeding experiment: 9 of 12 ribs, 2 of 12 vertebrae, 2 of 3 scapulae, 2 of 3 humeri, and 1 of 3 ulnae. Three radii and 6 carpals were undamaged. Gnawing by Hadza foragers prior to scavenger activity produced high frequencies of postcranial damage with almost 79% of dik-dik bones (54 ribs and 2 metapodials) broken (Oliver, 1993).

In a sample of capuchin monkeys roasted and eaten by Aché foragers, damage to most of the crania was similar to that seen in the Ngogo sample. In this sample, access to the brain left the face relatively intact with breaks along the sagittal suture and the braincase fragmented or missing (Nicholson, 2005: 41, Fig. 5.1). Tooth marks and chewing damage were not studied, but 33% of all monkey and coati long bone specimens (N = 73) were modified into bone cylinders for bone marrow access mainly by breakage with metal tools. Long bone cylinders with cut or sawed ends have been recognized as a human-induced damage pattern in other small mammal faunal assemblages (e.g., Jones, 1983; Gifford-Gonzalez, 1989; Hockett, 1991).

Central African Republic Bofi foragers boiled blue duikers, brush-tailed porcupines, and giant pouched rats they hunted, but they roasted the murid rats and mice over open flames (Landt, 2004). For all prey, frequencies of tooth-marked bone specimens ranged from 12.0% to 34.8%. Ribs, thoracic vertebrae, and innominates of all prey were the most often damaged during mastication (based on NISP counts). Unlike the Ngogo assemblage, in which 98% of the long bones were missing at least one epiphysis, very few long bones in the Bofi assemblages (2/119, 1%) were classified as true bone cylinders or had both ends removed yet retained some cancellous matrix (6/119, 5%). The remaining long bones were either complete, sometimes with minimal damage on the epiphyses (68/119, 57%), or exhibited midshaft breaks (43/119, 36%).

Clearly, boiling and pot-sizing strongly affect these human-modified samples likely resulting in the low frequency of damage on limb ends compared to the Ngogo assemblage. However, the above studies find a much higher overall proportion of tooth marking on human-chewed samples compared with Ngogo. More systematic studies of human mastication damage to small mammals, especially without the assistance of metal knives or boiling, would help demonstrate unique versus shared features of human and chimpanzee chewing damage patterns.

5. Synthesis. We did not set out to undertake a comprehensive comparative study of chimpanzee, raptor, and non-primate mammalian predator taphonomy of kill assemblages. Nonetheless, we note that there are salient differences in taphonomic kill signatures made by mammalian and avian predators. We focus here on raptors, leopards, and chimpanzees. Studies of modern human mastication damage to small prey are largely distinguishable by metal knife cut marks and traces of burning or boiling on bones; these are not described in detail here. Additionally, human bone modification of small prey tends to leave a much lower frequency of long bone cylinders than does chimpanzee mastication (6–38% in the former versus 98% in the latter; Landt, 2004; Nicholson, 2005; this study).

Studies of raptor predation on mammalian prey, particularly of crowned hawk-eagles killing cercopithecoid monkeys, show that they have a distinctive taphonomic signal. Their kill assemblages are generally comprised of materials that drop from their nests, representing the best chance for a substantial accumulation of bones. These remains are characterized by: a high survivability of cranial and limb elements, particularly hind limb bones (especially the femur and tibia); poor survivability of axial postcranial elements, small bones from the manus and pes, and clavicles; scapulae with raking damage to the vertebral border of the blade; long bones remaining largely whole except for occasional damage to epiphyseal ends; crania showing punctures, nicks, and "can-opener" perforations producing bony flaps; adult crania remaining essentially complete; subadult and juvenile crania frequently having the skull base (and sometimes the splanchnocrania) removed; infant crania disarticulated along sutural lines and frequently missing their facial elements; mandibles with a lower survival rate than crania (thus, not very many associated crania and dentaries); and cranial perforations concentrated in and around the orbits, laterally behind the orbits, and in the basicranium (Sanders et al., 2003; McGraw et al., 2006; Trapani et al., 2006). In addition, their kill assemblages usually are dominated by one type of animal—at Ngogo, Uganda, and Tai

Forest, Ivory Coast, these are small-medium-sized cercopithecoid monkeys, and in more open country settings the preferred prey is hyraxes (Cruz-Uribe and Klein, 1998; references in Sanders et al., 2003).

Leopards often stash prey in caves or in trees (de Ruiter and Berger, 2000), providing good opportunities for the accumulation of bone. Leopards fragment skeletal remains of their prey much more severely than do raptors. Their damage to adult crania of prey species is also more comprehensive—for example, the skulls of adult hyraxes killed and devoured by leopards have their anterior facial regions and mandibular corpora separated from the rest of the cranium and mandibular rami—and bones in these assemblages are frequently tooth-marked (Simons, 1966; Brain, 1981; Pickering et al., 2004; Trapani et al., 2006). Thus, even when mammalian predators such as leopards take prey of similar size to that hunted by raptors, and even though the resulting kill assemblages may be alike in terms of bone element survivorship, the resulting damage patterns are very distinctive.

Damage to monkey skeletons resulting from chimpanzee predation resembles both leopard and eagle assemblages in bone survivorship profiles but seems distinctive in: being skewed towards skeletal remains from immature individuals; exhibiting little tooth marking; and exhibiting less damage to long bone diaphyses than in other mammalian carnivores. Chimpanzees also do not seem to exhibit caching behavior or to carry their prey back to particular sites or sleeping nests, meaning that the remains of their kills are likely to be more scattered. Clearly, these comparisons are not exhaustive or extensive, but they are suggestive and encouraging that the involvement of specific classes of predators might be deciphered from fossil kill assemblages.

Applicability to fossil sites: cautions

It is currently not known if early hominins hunted. The results of this paper present a model that may be useful for detecting occasional early hominin carnivory. However, we caution against using this taphonomic model without the following considerations:

1. Human and chimpanzee hunting may not be homologous behaviors. Chimpanzee hunting does not necessitate small mammal hunting in the last common ancestor of humans and chimpanzees, nor in the earliest hominins.
2. Stone tools change how a carcass is processed. This taphonomic model may therefore only be applicable to pre-technological hominin sites.
3. These results derive from an occasionally arboreal hominoid hunting arboreal prey. The utility of this taphonomic model may be limited to hominins that were at least occasionally arboreal.
4. Hunting in modern chimps and modern hunter-gatherers is part of a broader dietary regime, and is also increasingly seen to play important social roles (e.g., as in models of costly signaling; Hawkes and Bliege Bird, 2002). Treatment of prey may have been quite different among earlier hominins with different dietary regimes where these social roles were different or absent altogether.
5. Preservation biases and the low likelihood of bone concentration may limit the direct comparison of these results to fossil assemblages.

Early hominin carnivory: the hard evidence

The earliest stone tool artifacts are from the 2.6 Ma site of Gona in the Afar region of Ethiopia (Semaw et al., 2003). Butchered ungulate bones have also been recovered from other 2.5–2.6 Ma sites at Gona (Domínguez-Rodrigo et al., 2005) and the nearby 2.5 Ma site of Bouri (de Heinzelin et al., 1999). These sites mark the origin of archaeologically visible large mammal carnivory by early hominins. This archaeological evidence is penecontemporaneous with the origin of the genus *Homo* at 2.3 Ma (Kimbel et al., 1996). However, most molecular estimates (Kumar and Hedges, 1998; Stauffer et al., 2001) and fossil evidence (Hailie-Selassie, 2001; Senut et al., 2001; Brunet et al., 2002) suggest that the hominin and chimpanzee lineages diverged at least six to eight million years ago. Therefore, there is considerable time during which the human lineage potentially was practicing some degree of pre-stone tool carnivory that may be difficult to detect in the archaeological record.

Chimpanzees as a model for pre-technological hominins

There is considerable debate as to whether Oldowan hominins relied more on hunting or on scavenging medium to large mammalian prey (e.g., Bunn and Ezzo, 1993; Blumenschine, 1995; Domínguez-Rodrigo, 2002; Domínguez-Rodrigo and Pickering, 2003). However, less prevalent in the zooarchaeological literature are taphonomic test criteria for recognizing early hominin hunting and consumption of small prey. Chimpanzee dietary behavior can inform this argument because although chimpanzees have been observed to occasionally scavenge (Hasegawa et al., 1983; Nishida, 1994; Muller et al., 1995), they acquire most of their meat by hunting (Uehara, 1997; Stanford, 1998; Mitani and Watts, 1999; Boesch and Boesch-Achermann, 2000), and therefore may provide an example of the bony assemblage produced by a primate that hunts small-sized vertebrate prey.

Although they have been observed to utilize stone artifacts (Boesch and Boesch, 1983) that can accumulate over time (Mercader et al., 2002), chimpanzees do not use stone tools to butcher animal prey. While a single chimpanzee has been observed to use a stick to pry a single squirrel out of its tree hole (Huffman and Kalunde, 1993), and another was observed to use a stick tool to extract marrow after the removal of a long bone epiphysis (Boesch and Boesch, 1989), chimpanzees do not typically use any form of technology during their hunting or feeding bouts.

Additionally, several early hominin specimens, including a pre-Oldowan Hadar fossil, have been estimated to have a bite force equivalent to that of modern apes (Demes and Creel, 1988). Therefore, if pre-stone tool-using hominins

processed small prey in a manner similar to chimpanzees, we would expect to find similar patterns of chewing damage on that prey. Chimpanzees and humans are unique among mammalian predators in their frequent removal of limb bone ends via chewing in order to suck out the marrow without always fragmenting the limb shafts. This also makes it reasonable to suggest that chimpanzees may provide a good model for the damage expected on bones modified by pre-stone tool-using hominins. However, as some early hominins (such as *Orrorin*) do not possess some of the unique dental traits of chimpanzees, which may be adaptations to meat-eating, they may not have incorporated meat into their diet on the same scale as do chimpanzees (Pickford, 2005).

Finally, pre-technological hominins were similar in body size to modern chimpanzees (McHenry, 1992), lived in more closed environments than later hominins (WoldeGabriel et al., 1994; Pickford and Senut, 2001; WoldeGabriel et al., 2001; Vignaud, et al., 2002), and may have retained some tree-climbing adaptations (Richmond, 1998; Hailie-Selassie, 2001; Senut et al., 2001; Ward, 2002). We suggest that if pre-stone tool-using Pliocene hominins hunted and consumed small sized prey, the taphonomic signature of that hunting behavior would be more similar to chimpanzee consumption of small prey than Oldowan hominin stone tool-assisted butchery of larger prey.

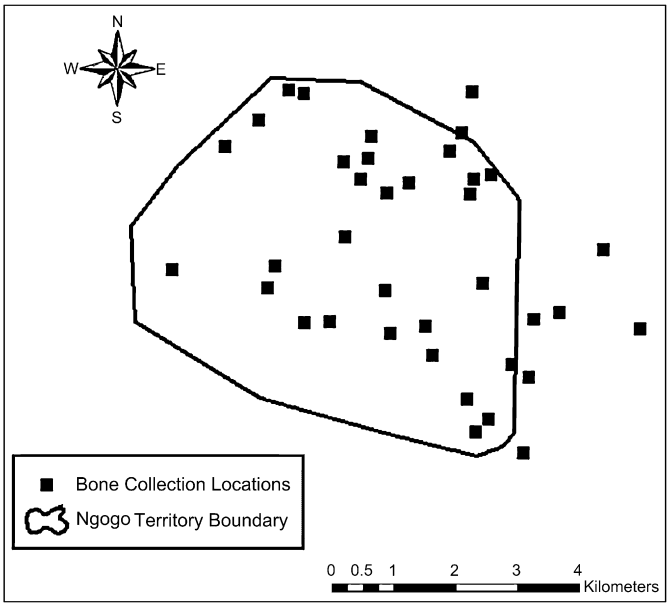

Fig. 15. Map of 37 bone collection sites throughout the Ngogo chimpanzee territory. The bones are scattered throughout the ~20 km^2. The random distribution of bony refuse makes it likely that this collection would be archaeologically invisible.

Preservation biases

There is a bias against animals weighing less than 15 kg accumulating in modern surface bone assemblages (Behrensmeyer et al., 1979). Not only are bones from smaller animals less likely to accumulate, but they are also less likely to preserve (Gordon and Buikstra, 1981). This could affect red colobus monkey prey remains, as adults generally weigh only 7.0–12.5 kg (Kingdon, 1974).

An additional problem is the preservation potential, or lack thereof, of some of these bone modification patterns. For instance, it can be difficult to document patterns of crenulation on fossil long bone ends. This is especially true in samples that are derived from hard breccia and prepared mechanically versus those prepared in acid, since this technique tends to leave breccia occupying the ends of broken long bones (D. deRuiter, pers. comm.). Still, we expect that skeletal element profiles and more gross damage, such as removal of long bone ends, will be preserved even if more detailed damage is not.

Is this set of bone specimens a true ''assemblage'' or a ''collection'' derived from a larger area than most fossil assemblages? In prehistoric studies, an assemblage is generally something that is all found in the same place, regardless of its level of autochthony. The likelihood that bone specimens derived from chimpanzee hunts will be first concentrated, and then buried, is low. The bony refuse left behind by the Ngogo chimpanzees after hunting was scattered throughout their 20 km^2 territory (Fig. 15). Because of the highly dispersed distribution of bone remains, this collection would most likely be archaeologically invisible. We argue that applying the taphonomic test criteria outlined here to assemblages with low time averaging from a single locality is important. Treating mixed assemblages as a single sample will invariably affect data such as prey size range, prey age distribution, skeletal element representation, and damage patterns. This would make comparisons between the Ngogo chimpanzee kill assemblage and fossil assemblages less useful.

Arboreal predators hunting arboreal prey

The taphonomic signals outlined here can only be confidently extrapolated to an at least occasionally arboreal hominin hunting arboreal prey. We do not know if or how terrestriality of predator or prey species might change some of the taphonomic signals in the prey assemblage. We suspect that the degree of terrestriality at least partially dictates what species are usually taken by a predator. It would be far less likely to find small- and medium-sized monkeys in the kill sample of a committed terrestrial predator (an obligate biped such as *Homo erectus*) because of the ability of the monkeys to escape into trees. The question of how arboreally adept late Pliocene hominins might have been, and thus how proficient they were at catching and killing agile monkeys in woodland and forest settings, remains open. Early Pleistocene, fully bipedal, stone-tool-wielding hominins living in wooded to open savannas are unlikely to have been fast enough to run down small, agile animals. But they could fill a niche of consuming meat and marrow from long bones of carcasses of large to very large animals, some of which were inaccessible even to hyaenids. This seems to have been the case at many of the earliest sites with butchered bones (e.g., de Heinzelin et al., 1999; Domínguez-Rodrigo et al., 2005).

Therefore, to maximize comparability of behavioral and ecological contexts when examining collections for these taphonomic signals, we suggest focusing on assemblages prior to the anatomical evidence for hominin obligate terrestriality. Although the degree to which early hominins were arboreal is currently unresolved, it is reasonable to suggest from the anatomy of the earliest hominins that they were at least occasionally in the trees (Richmond, 1998; Hailie-Selassie, 2001; Senut et al., 2001; Ward, 2002). We also suggest investigating sites with environments reconstructed as more wooded and wet with the trees necessary for arboreal monkeys and at least partially arboreal hominins, and particularly those sites where hominins and colobine monkeys co-occur. While it has been suggested that some larger-bodied early Pliocene colobines were predominantly terrestrial (Harris et al., 2003; Leakey et al., 2003), more recent analysis of the largest early Pliocene colobine indicates that this species, and the majority of early Pliocene colobines, were in fact arboreal (Hlusko, 2006).

The two earliest hominin sites—the *Sahelathropus tchadensis* site of Toros-Menalla, Chad (at about 6–7 Ma), and the *Orrorin tugenensis* site of Kapsomin, Tugen Hills, Kenya (at about 6 Ma)—included gallery forest components, and fossil evidence for the presence of colobus monkeys has been found at these sites (Pickford and Senut, 2001; Vignaud, et al., 2002). The colobine remains from Toros-Menalla is a single damaged maxilla (Vignaud et al., 2002), but the faunal assemblage from Kapsomin is dominated by small to medium ruminants and colobine monkeys that Pickford and Senut (2001) interpret to be the prey remains of a leopard-like cat. *Ardipithecus ramidus kadabba* specimens from the Central Awash Complex (at 5.54–5.77 Ma) were deposited in a wooded and possibly humid environment (WoldeGabriel et al., 2001). The fauna associated with *Ardipithecus ramidus* from Aramis, Ethiopia (at 4.4 Ma) is dominated by colobine monkeys (over 30% of all identifiable vertebrates in the assemblage) in a closed, wooded environment (WoldeGabriel et al., 1994). *Australopithecus anamensis* specimens from Asa Issie (at 4.1–4.2 Ma) were also deposited in a wooded environment, and the fauna is heavily dominated by cercopithecid primates (just under 50% of all identifiable macrovertebrates; White et al., 2006).

The skeletal element profiles of colobine monkeys from these sites have not been published, but these hominin-colobine co-occurrences are intriguing. Taphonomic damage to these colobines is also currently uninvestigated or unpublished. The only exception is a description of carnivore damage on two different humeri (a proximal humerus and an upper and middle humerus shaft) of *Kuseracolobus hafu*, a large colobine monkey from Asa Issie (Hlusko, 2006).

Summary and conclusions

We present a taphonomic analysis of the largest collection of the remains of primates hunted by chimpanzees to date. This study confirms some of the taphonomic patterns described in an earlier study analyzing a much smaller sample (Plummer and Stanford, 2000). The taphonomic signature of chimpanzee kills includes a focus on colobus monkeys, an age profile skewed towards pre-adults, and a skeletal element profile dominated by cranial fragments (but with no complete crania) followed by long bones, and lacking pre-caudal vertebrae. A high proportion of limb bones had their epiphyses chewed off, leaving intact metaphyses with gnawed ends. We also documented chimpanzee-specific types of damage in this collection, including: relatively low tooth mark frequencies (4.4% of total NISP); compression cracking of the crania; innominates reduced to only ilia; and transverse incipient breaks on the ribs. When compared to collections of primate remains modified by other agents, including leopards and eagles, there are similarities, especially with skeletal element profiles of leopard assemblages, but damage patterns and age profiles remain distinctive. Reports of damage to bones by modern humans indicate that the Ngogo sample may be a good model for the kinds of damage early hominins may have inflicted on small mammal prey, since they are loosely similar in their craniodental anatomy and biomechanics.

We agree with Pickering and Wallis (1997) that we should not automatically assign all non-hominin masticatory damage traces in archaeofaunas to carnivores. We disagree, however, with their conclusions regarding the degree of similarity between hominoid and carnivore bone modification. Although Pickering and Wallis (1997) recognized that their sample was limited in its breadth and focused only on bone modifications, we believe that we have illustrated significant differences between bones modified by these different agents using a diversity of taphonomic variables. A broad approach, taking into account not only bone modification patterns but also prey size, skeletal element profiles, and age distribution of a fossil assemblage should help to identify the prehistoric predator(s) responsible for the creation and modification of a fossil assemblage. However, there is a strong possibility that some of these patterns, including specific damage patterns and even skeletal or age profiles, may become obscured by subsequent taphonomic processes affecting the assemblage. This is likely to happen, at varying degrees, to most fossil assemblages. Additionally, it may be difficult to identify small primate cranial fragments or ribs, rendering skeletal element profiles less useful for comparative analyses. Furthermore, small animals are less likely to be preserved in the fossil record, rendering these patterns less archaeologically visible.

We are not advocating applying this taphonomic model wholesale to identify hominin hunting of small prey at sites post-dating the advent of stone tool technology, at about 2.5 Ma (Semaw et al., 1997). Presumably, once hominins were using stone tools, they almost certainly processed carcasses in different ways. We also want to underscore the uniqueness of Oldowan hominin consumption of terrestrial prey, which included procuring animals larger than the predator, at least sometimes incorporated tool use, and may have incorporated complex vocal communication and bipedalism into prey acquisition and processing (Butynski, 1982). We think the most appropriate fossil samples to examine for these taphonomic variables are those in which early hominins are found with a relatively large sample of cercopithecoids in a wetter, more wooded, or forest environment. A closer

inspection of the taphonomy of cercopithecoid remains from these sites is the first step towards possibly documenting early hominin hunting in an arboreal setting.

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References

Andrews, P., 1990. Owls, Caves and Fossils. University of Chicago Press, Chicago.

Andrews, P., Nesbit-Evans, E.M., 1983. Small mammal bone accumulations produced by mammalian carnivores. Paleobiology 9, 289–307.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4, 150–162.

Behrensmeyer, A.K., Western, D., Dechant-Boaz, D., 1979. New perspectives in vertebrate paleoecology from a recent bone assemblage. Paleobiology 5, 12–21.

Berger, L.R., Clarke, R.J., 1995. Eagle involvement in accumulation of the Taung child fauna. J. Hum. Evol. 29, 275–299.

Binford, L.R., 1978. Nunamiut Ethnoarchaeology. Academic Press, New York.

Binford, L.R., 1981. Bones: Ancient Men and Modern Myths. Academic Press, New York.

Blumenschine, R.J., 1986. Early Hominid Scavenging Opportunities: Implications of Carcass Availability in the Serengeti and Ngorongoro Ecosystems. In: BAR International Series, 283. Oxford.

Blumenschine, R.J., 1995. Percussion marks, tooth marks and the experimental determinations of the timing of hominid and carnivore access to long bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. J. Hum. Evol. 29, 21–51.

Blumenschine, R.J., Marean, C.W., Capaldo, S.D., 1996. Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. J. Archaeol. Sci. 23, 493–507.

Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. Nature 333, 763–765.

Blumenschine, R.J., Selvaggio, M.M., 1991. On the marks of marrow bones by hammerstones and hyenas: their anatomical patterning and archaeological implication. In: Clark, J.D. (Ed.), Cultural Beginnings: Approaches to Understanding Early Hominid Lifeways in the African Savannah. Dr. Rudolf Habelt, GMBH, Bonn, pp. 17–32.

Boesch, C., Boesch, H., 1983. Optimisation of nut-cracking with natural hammers by wild chimpanzees. Behaviour 83, 265–286.

Boesch, C., Boesch, H., 1989. Hunting behavior of wild chimpanzees in the Taï National Park. Am. J. Phys. Anthropol. 78, 547–573.

Boesch, C., Boesch-Achermann, H., 2000. The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution. Oxford University Press, New York.

Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. University of Chicago Press, Chicago.

Brown, L.H., 1971. The relations of the crowned eagle *Stephanoaetus coronatus* and some of its prey animals. Ibis 113, 240–243.

Brunet, M., Guy, F., Pilbeam, D., Mackaye, H.T., Likius, A., Ahounta, D., Alain Beauvilain, A., Blondel, C., Bocherens, H., Renaud Boisserie, R., De Bonis, L., Coppens, Y., Dejax, J., Denys, C., Duringer, P., Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Campomanes, P.P., Ponce De Leon, M., Rage, J.-C., Sapanet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A., Zollikofer, C., 2002. A new hominid from the Upper Miocene of Chad, Central Africa. Nature 418, 145–151.

Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. Nature 291, 547–577.

Bunn, H.T., 1982. Meat-eating and human evolution: studies of the diet and subsistence patterns of Plio-Pleistocene hominids. Ph.D. Dissertation, University of California, Berkeley.

Bunn, H.T., Ezzo, J.A., 1993. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioral implications. J. Archaeol. Sci. 20, 365–398.

Butynski, T., 1982. Vertebrate predation by primates: a review of hunting patterns and prey. J. Hum. Evol. 11, 421–430.

Capaldo, S.D., Blumenschine, R.J., 1994. A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing on bovid long bones. Am. Antiq. 59, 724–748.

Carlson, K.J., Pickering, T.R., 2003. Intrinsic qualities of primate bones as predictors of skeletal element representation in modern and fossil carnivore feeding assemblages. J. Hum. Evol. 44, 431–450.

Carlson, K.J., Pickering, T.R., 2004. Shape-adjusted bone mineral density measurements in baboons: other factors explain primate skeletal element representation at Swarktrans. J. Archaeol. Sci. 31, 577–583.

Cruz-Uribe, K., Klein, R.G., 1998. Hyrax and hare bones from modern South African eagle roosts and the detection of eagle involvement in fossil bone assemblages. J. Archaeol. Sci. 25, 135–147.

Demes, B., Creel, N., 1988. Bite force, diet, and cranial morphology of fossil hominids. J. Hum. Evol. 17, 657–670.

de Heinzelin, J., Clark, J.D., White, T., Hart, W., Renne, P., WoldeGabriel, G., Beyene, Y., Vrba, E., 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. Science 284, 625–629.

de Ruiter, D.J., Berger, L.R., 2000. Leopards as taphonomic agents in dolomitic caves – implications for bone accumulations in the hominid-bearing deposits of South Africa. J. Archaeol. Sci. 27, 665–684.

Domínguez-Rodrigo, M., 2002. Hunting and scavenging by early humans: the state of the debate. J. World Prehist. 16, 1–54.

Domínguez-Rodrigo, M., Pickering, T.R., 2003. Early hominid hunting and scavenging: a zooarchaeological review. Evol. Anthropol. 12, 275–282.

Domínguez-Rodrigo, M., Pickering, T.R., Semaw, S., Rogers, M.J., 2005. Cut-marked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for the functions of the world's oldest stone tools. J. Hum. Evol. 48, 109–121.

Eickhoff, S., Herrmann, B., 1985. Surface marks on bones from a Neolithic collection grave (Odagsen, Lower Saxony): a study on differential diagnosis. J. Hum. Evol. 14, 263–274.

Elkin, D., Mondini, M., 2001. Human and small carnivore gnawing damage on bones – an exploratory study and its archaeological implications. In: Mondini, M. (Ed.), Ethnoarchaeology of Andean South America. International Monographs in Prehistory, Lawrence A, Kuznar, pp. 255–265.

Fisher Jr., J.W., 1995. Bone surface modifications in zooarchaeology. J. Archaeol. Method Theory 2, 7–68.

Gifford-Gonzalez, D., 1989. Ethnographic analogues for interpreting modified bones: some cases from East Africa. In: Bonnichsen, R., Sorg, M.H. (Eds.), Bone Modification. Center for the Study of the First Americans, Orono, Maine, pp. 179–246.

Gordon, C.C., Buikstra, J.E., 1981. Soil pH, bone preservation, and sampling bias at mortuary sites. Am. Antiq. 46, 566–571.

Hailie-Selassie, Y., 2001. Late Miocene hominids from the Middle Awash, Ethiopia. Nature 412, 178–181.

Harris, J.M., Leakey, M.G., Cerling, T.E., 2003. Early Pliocene tetrapod remains from Kanapoi, Lake Turkana Basin, Kenya. In: Harris, J.M.,

Leakey, M.G. (Eds.), Geology and Vertebrate Paleontology of the Early Pliocene Site of Kanapoi, Northern Kenya. Natural History Museum of Los Angeles County, Contributions in Science, 498, pp. 39–113.

Hasegawa, T., Miraiwa, M., Nishida, T., Takasaki, H., 1983. New evidence on scavenging behavior in wild chimpanzees. Curr. Anthropol. 24, 231–232.

Hawkes, K., Bliege Bird, R., 2002. Showing-off, handicap signaling, and the evolution of men's work. Evol. Anthropol. 11, 58–67.

Haynes, G., 1980. Evidence of carnivore gnawing on Pleistocene and recent mammalian bones. Paleobiology 6, 341–351.

Haynes, G., 1982. Utilization and skeletal disturbances of North American prey carcasses. Artic 35, 266–281.

Haynes, G., 1983. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. Paleobiology 9, 164–172.

Hlusko, L.J., 2006. A new large Pliocene colobine species (Mammalia: Primates) from Asa Issie, Ethiopia. Geobios 39, 57–69.

Hockett, B.S., 1991. Towards distinguishing human and raptor patterning on leporid bones. Am. Antiq. 56, 667–679.

Huffman, M.A., Kalunde, M.S., 1993. Tool-assisted predation on a squirrel by a female chimpanzee in the Mahale Mountains, Tanzania. Primates 34, 93–98.

Johnson, E., 1985. Current developments in bone technology. In: Bonnichsen, R., Sorg, M.H. (Eds.), Bone Modification. Center for the Study of the First Americans, Orono, Maine, pp. 431–471.

Jones, K.T., 1983. Foraging archaeology: the Ache of Eastern Paraguay. In: Lemoyne, G.M., MacEachern, A.S. (Eds.), Carnivores, Human Scavengers, and Predators: A Question of Bone Technology. Archaeological Association, University of Calgary, pp. 171–191.

Kawanaka, K., 1982. Further studies on predation by chimpanzees of the Mahale Mountains. Primates 23, 364–384.

Kimbel, W.H., Walter, R.C., Johanson, D.C., Reed, K.E., Aronson, J.L., Assefa, Z., Marean, C., Eck, G.G., Bobe, R., Hovers, E., Rak, Y., Vondra, C., Yemane, T., York, D., Chen, Y., Evensen, N.M., Smith, P.E., 1996. Late Pliocene Homo and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. J. Hum. Evol. 31, 549–561.

Kingdon, J., 1974. East African Mammals, vol. 1. University of Chicago Press, Chicago.

Kumar, S., Hedges, S.B., 1998. A molecular timescale for vertebrate evolution. Nature 392, 917–920.

Landt, M.J., 2004. Investigations of human gnawing on small mammal bones among contemporary Bofi foragers of the Central African Republic. M.A. Thesis, Washington State University.

Leakey, M.G., Teaford, M.F., Ward, C.V., 2003. Cercopithecidae from Lothagam. In: Leakey, M.G., Harris, J.M. (Eds.), Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York, pp. 201–248.

Lyman, R.L., 1994. Vertebrate Taphonomy. Cambridge University Press, Cambridge.

Maguire, J.M., Pemberton, D., Collett, H.M., 1980. The Makapansgat Limeworks grey breccia: hominids, hyaenas, hystricids or hillwash? Paleontol. Afr. 23, 75–98.

Marshall, L.G., 1989. Bone modification and the ''laws of burial''. In: Bonnichsen, R., Sorg, M.H. (Eds.), Bone Modification. Center for the Study of the First Americans, Orono, Maine, pp. 7–24.

McGraw, W.S., Cooke, C., Shultz, S., 2006. Primate remains from African crowned eagle (*Stephanoaetus coronatus*) nests in Ivory Coast's Tai Forest: implications for primate predation and early hominid taphonomy in South Africa. Am. J. Phys. Anthropol. 131, 151–165.

McHenry, H., 1992. Body size and proportions in early hominids. Am. J. Phys. Anthropol. 87, 407–431.

Mercader, J., Panger, M., Boesch, C., 2002. Excavation of a chimpanzee stone tool site in the African rainforest. Science 296, 1452–1455.

Mitani, J.C., Merriwether, D.A., Zhang, C., 2000. Male affiliation, cooperation and kinship in wild chimpanzees. Anim. Behav. 59, 885–893.

Mitani, J.C., Watts, D.P., 1999. Demographic influences on the hunting behavior of chimpanzees. Am. J. Phys. Anthropol. 109, 439–454.

Mitani, J.C., Watts, D.P., 2001. Why do chimpanzees hunt and share meat? Anim. Behav. 61, 915–924.

Mitani, J.C., Watts, D.P., Lwanga, J., 2002. Ecological and social correlates of chimpanzee party size and composition. In: Boesch, C., Hohmann, G., Marchant, L.F. (Eds.), Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp. 102–111.

Muller, M.N., Mpongo, E., Stanford, C.B., Boehm, C., 1995. A note on scavenging by wild chimpanzees. Folia Primatol. 65, 43–47.

Newton-Fisher, N.E., Notman, H., Reynolds, V., 2002. Hunting of mammalian prey by Budongo forest chimpanzees. Folia Primatol. 73, 281–283.

Nicholson, C.M., 2005. Small-game utilization among the Aché of eastern Paraguay: a study of taphonomy in ethnoarchaeology. M.A. Thesis, Washington State University.

Nishida, T., 1994. Review of recent findings on Mahale chimpanzees: implications and future research directions. In: Wrangham, R.W., McGrew, W.C., de Waal, F.B.M., Heltne, P.G. (Eds.), Chimpanzee Cultures. Harvard University Press, Cambridge, pp. 373–396.

Nishida, T., Uehara, S., Nyundo, R., 1979. Predatory behavior among wild chimpanzees of the Mahale mountains. Primates 20, 1–20.

Oliver, J.S., 1993. Carcass processing by the Hadza: bone breakage from butchery to consumption. In: Hudson, J. (Ed.), From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains. Center for Archaeological Investigations, Southern Illinois University at Carbondale, Occasional Paper No. 21, pp. 200–227.

Pickering, T.R., 2001a. Taphonomy of the Swartkrans hominid postcrania and its bearing on issues of meat-eating and fire management. In: Stanford, C.B., Bunn, H.T. (Eds.), Meat-Eating and Human Evolution. Oxford University Press, Oxford, pp. 33–51.

Pickering, T.R., 2001b. Carnivore voiding: a taphonomic process with the potential for the deposition of forensic evidence. J. Forensic Sci. 46, 406–411.

Pickering, T.R., Carlson, K.J., 2002. Baboon bone mineral densities: implications for the taphonomy of primate skeletons in South African cave sites. J. Archaeol. Sci. 29, 883–896.

Pickering, T.R., Domínguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2004. Beyond leopards: tooth marks and the contribution of multiple carnivore taxa to the accumulation of the Swartkrans Member 3 fauna. J. Hum. Evol. 46, 595–604.

Pickering, T.R., Wallis, J., 1997. Bone modifications resulting from captive chimpanzee mastication: implications for the interpretation of Pliocene archaeological fauna. J. Archaeol. Sci. 24, 1115–1127.

Pickford, M., 2005. Incisor-molar relationships in chimpanzees and other hominoids: implications for diet and phylogeny. Primates 46, 21–32.

Pickford, M., Senut, B., 2001. The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. Comptes Rendus de l'Academie des Sciences- Series IIA 332, 145–152.

Plummer, T.W., Stanford, C.B., 2000. Analysis of a bone assemblage made by chimpanzees at Gombe National Park, Tanzania. J. Hum. Evol. 39, 345–365.

Potts, R.B., 1988. Early Hominid Activities at Olduvai. Aldine de Gruyter, New York.

Potts, R.B., Shipman, P., 1981. Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. Nature 291, 577–580.

Richmond, B.R., 1998. Ontogeny and biomechanics of phalangeal form in primates. Ph.D. Dissertation, State University of New York, Stony Brook.

Sanders, W.J., Trapani, J., Mitani, J.C., 2003. Taphonomic aspects of crowned hawk-eagle predation on monkeys. J. Hum. Evol. 44, 87–105.

Schultz, A.H., 1961. Vertebral column and thorax. In: Hofer, H., Schultz, A.H., Starck, D. (Eds.), Primatologia, vol. 4, no. 4. Karger, Basel.

Semaw, S., Renne, P., Harris, J.W.K., Feibel, C.S., Bernor, R.L., Fesseha, N., Mowbray, K., 1997. 2.5-million-year-old stone tools from Gona, Ethiopia. Nature 385, 333–336.

Semaw, S., Rogers, M.J., Quade, J., Renne, P.R., Butler, R.F., Dominguez-Rodrigo, M., Stout, D., Hart, W.S., Pickering, T., Simpson, S.W., 2003. 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. J. Hum. Evol. 45, 169–177.

Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., Coppens, Y., 2001. First hominid from the Miocene (Lukeino Formation, Kenya). Comptes Rendus de l'Academie des Sciences—Series IIA 332, 137–144.

Shipman, P., 1981. Life History of a Fossil: An Introduction to Taphonomy and Paleoecology. Harvard University Press, Cambridge.

Shipman, P., Bosler, W., Davis, K.L., 1981. Butchering of giant geladas at an Acheulean site. Curr. Anthropol. 22, 257–286.

Shipman, P., Rose, J., 1983. Early hominid hunting, butchering and carcass-processing behaviors: approaches to the fossil record. J. Anthropol. Archaeol. 2, 57–98.

Simons, J.W., 1966. The presence of leopard and a study of the food debris in the leopard lairs of the Mount Suswa Caves, Kenya. Bulletin of the Cave Exploration Group of East Africa 1, 51–69.

Stanford, C.B., 1996. The hunting ecology of wild chimpanzees: implications for the behavioral ecology of Pliocene hominids. Am. Anthropol. 98, 96–113.

Stanford, C.B., 1998. Chimpanzee and Red Colobus: The Ecology of Predator and Prey. Harvard University Press, Cambridge.

Stanford, C.B., 1999. The Hunting Apes: Meat-eating and the Origins of Human Behavior. Princeton University Press, Princeton.

Stauffer, R.L., Walker, A., Ryder, O.A., Lyons-Weiler, M., Blair Hedges, S., 2001. Human and ape molecular clocks and constraints on paleontological hypotheses. J. Heredity 92, 469–474.

Stern, M., Goldstone, R., 2005. Red colobus as prey: the leaping habits of five sympatric old world monkeys. Folia Primatol. 76, 100–112.

Struhsaker, T.T., 1975. The Red Colobus Monkey. University of Chicago Press, Chicago.

Strum, S.C., 1981. Processes and products of change: baboon predatory behavior at Gilgil, Kenya. In: Harding, R.S.O., Teleki, G. (Eds.), Omnivorous Primates: Gathering and Hunting in Human Evolution. Columbia University Press, New York, pp. 255–302.

Strum, S.C., 1983. Baboon cues for eating meat. J. Hum. Evol. 12, 327–336.

Swindler, D.R., Wood, C.D., 1982. An Atlas of Primate Gross Anatomy. Robert E. Krieger Publishing Company, Malabar, Florida.

Takahata, Y., Hasegawa, T., Nishida, T., 1984. Chimpanzee predation in the Mahale Mountains from August 1979 to May 1982. Int. J. Primatol. 5, 213–233.

Tappen, M., Wrangham, R., 2000. Recognizing hominoid-modified bones: the taphonomy of colobus bones partially digested by free-ranging chimpanzees in the Kibale forest, Uganda. Am. J. Phys. Anthropol. 118, 217–234.

Teleki, G., 1973. The Predatory Behavior of Wild Chimpanzees. Bucknell University Press, Lewisburg, PA.

Trapani, J., Sanders, W.J., Mitani, J.C., Heard, A., 2006. Precision and consistency of the taphonomic signature of predation by crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. Palaios 21, 114–131.

Uehara, S., 1997. Predation on mammals by the chimpanzee (*Pan troglodytes*). Primates 38, 193–214.

Vignaud, P., Duringer, P., Mackaye, H.T., Likius, A., Blondel, C., Boisserie, J.-R., de Bonis, L., Eisenmann, V., Etienne, M.-E., Geraads, D., Guy, F., Lehmann, T., Lihoreau, F., Lopez-Martinez, N., Mourer-Chauviré, C., Otero, O., Rage, J.-C., Schuster, M., Viriot, L., Zazzo, A., Brunet, M., 2002. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. Nature 418, 152–155.

Ward, C.V., 2002. Interpreting the posture and locomotion of *A. afarensis*: where do we stand? Yearb. Phys. Anthropol. 45, 185–215.

Watts, D.P., Mitani, J.C., 2002. Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. Int. J. Primatol. 23, 1–28.

Weisler, M.I., Gargett, R.H., 1993. Pacific island avian extinctions: the taphonomy of human predation. Archaeology in Oceania 28, 85–93.

White, T.D., 1992. Human Osteology. Academic Press, San Diego.

White, T.D., WoldeGabriel, G., Asfaw, B., Ambrose, S., Beyene, Y., Bernor, R.L., Boisserie, J.-R., Currie, B., Gilbert, H., Haile-Selassie, Y., Hart, W.K., Hlusko, L.J., Howell, F.C., Kono, R.T., Lehmann, T., Louchart, A., Lovejoy, C.O., Renne, P.R., Saegusa, H., Vrba, E.S., Wesselman, H., Suwa, G., 2006. Asa Issie, Aramis and the origins of *Australopithecus*. Nature 440, 883–889.

WoldeGabriel, G., Haile-Selassie, Y., Renne, P.R., Hart, W.K., Ambrose, S.H., Asfaw, B., Heiken, G., White, T., 2001. Geology and palaeontology of the Late Miocene Middle Awash valley, Afar rift, Ethiopia. Nature 412, 175–178.

WoldeGabriel, G., White, T.D., Suwa, G., Renne, P., de Heinzelin, J., Hart, W.K., Heiken, G., 1994. Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. Nature 371, 330–333.