



# Taphonomic Aspects of Crowned Hawk-Eagle Predation on Monkeys

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## Abstract

This study provides a taphonomic analysis of prey accumulations of crowned hawk-eagles (*Stephanoaetus coronatus*) from Ngogo, Kibale National Park, Uganda, collected over 37 months from below nests of two eagle pairs. Crowned hawk-eagles are powerful predators capable of killing animals much larger than themselves, and are significant predators of cercopithecoid monkeys in forest habitats throughout sub-Saharan Africa. At Ngogo, 81% of the individuals in the kill sample are monkeys. Redtail monkeys (*Cercopithecus ascanius*) are particularly well represented in the sample, making up 66% of monkeys identified to species. Despite an impressive killing apparatus, crowned hawk-eagles are fastidious eaters that inflict far less damage to bone than mammalian predators. Examination of skeletal material from the Ngogo kill sample reveals that crania, hindlimb elements, and scapulae survive predation better than do other bones. Crania of adults are typically complete and accompanied by mandibles, while crania of young individuals are usually dissociated from mandibles and lack basicrania and faces. Long bones are often whole or show minimal damage. Thin bones, such as crania and innominates, are marked by numerous nicks, punctures, and “can-opener” perforations. Scapular blades are heavily raked and shattered. Along with the strong preference for cercopithecoids, these distinct patterns of bone survival and damage indicate the feasibility of recognizing specific taphonomic signatures of large raptors in fossil assemblages.

Berger and Clarke (1995) hypothesized that crowned hawk-eagles or similar large raptors were principally responsible for the accumulation of the late Pliocene fossil fauna from Taung, South Africa, including the type infant skull of *Australopithecus africanus*. The results of our study suggest that the faunal composition and type of damage to the hominid skull and other bone from Taung are consistent with the predatory activities of large raptors. More rigorous assessment of their hypothesis will require sorting the Taung fauna by locality and further detailed analysis of species composition and bone damage and survivability patterns.

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## Introduction

Crowned hawk-eagles (*Stephanoaetus coronatus*) are large (weight, 3.4–4.1 kg; length, 81–92 cm), immensely powerful raptors (Steyn, 1973; Williams and Arlott, 1980; Brown et al., 1982). Armed with deep, well-curved beaks, thick legs, robust toes, and long, sharp talons that are reportedly stronger than those of any other African eagle, they are voracious predators of small-to-medium-sized mammals, and can kill animals as large as bushbuck (ca. 30 kg) (Brown, 1971; Steyn, 1973; Daneel, 1979; Brown et al., 1982; Steyn, 1983). They are significant predators of cercopithecoid monkeys throughout sub-Saharan Africa (Skorupa, 1989; Struhsaker and Leakey, 1990; Leland and Struhsaker, 1993; Maisels et al., 1993; Hart et al., 1996; Mitani et al., 2001), a fact attested to by the variety and intensity of mechanisms used by monkeys to deter predation by these raptors, including loud calls, tightened grouping of troop members, rapid descent through the canopy, and aggressive defensive behavior (Gautier-Hion and Tutin, 1988; Cordeiro, 1992; Maisels et al., 1993).

In this paper we provide a taphonomic interpretation of prey assemblages accumulated by crowned hawk-eagles living in the Ngogo study area in Kibale National Park, Uganda and collected at their nests over a period of 37 months (Mitani et al., 2001). Eight diurnal anthropoid species are present at Ngogo and elsewhere in Kibale National Park, including a hominoid (chimpanzees, *Pan troglodytes*), two colobines (black and white colobus, *Colobus guereza*, and red colobus, *Piliocolobus badius*), and five cercopithecines (redtail monkeys, *Cercopithecus ascanius*, blue monkeys, *C. mitis*, l'Hoest's monkeys, *C. lhoesti*, olive baboons, *Papio anubis*, and grey-cheeked mangabeys, *Lophocebus albigena*) (Leland and Struhsaker, 1987; Struhsaker and Leakey, 1990; Mitani et al., 2000, 2001; Mitani and Watts, 2001). As primates, particularly cercopithecoids, compose a large percentage of the mammalian biomass in the 12 km<sup>2</sup> Ngogo area (Struhsaker, 1997), it is not surprising that monkeys dominate the resident crowned hawk-eagle kill sample (Mitani et al., 2001).

Recently, crowned hawk-eagles were implicated as possible accumulators of the faunal assemblage from the late Pliocene site of Taung, South Africa (Berger and Clarke, 1995), which includes cercopithecoid bones and the infant type skull of *Australopithecus africanus* (Cooke, 1990). Results of our analysis have important implications for this and other such hypotheses. Along with showing a strong preference by resident crowned hawk-eagles for cercopithecoids, skeletal analysis of the Ngogo kill aggregation reveals distinct patterns of bone survival and damage. These findings indicate the feasibility of recognizing specific taphonomic signatures of large raptors in fossil assemblages.

## Sample and methods

The kill sample was collected between July 1996 and August 1999 from below the nests of two pairs of crowned hawk-eagles. Details about nestlings and fledglings associated with each nest are reported in Mitani et al. (2001). Searches at the first nest (Nest A) were conducted approximately once a week during nestling phases and periods of eaglet dependence, and at other times bi-weekly. The second nest (Nest B) was discovered in June 1999 and monitored bi-weekly over three months. Searches involved comprehensive, diligent, and repetitive surface collecting. Material was not screened, but many small bones and bone fragments were collected. Because of the diligence of the searches for prey remains and collecting under the nests, it is likely that the study sample accurately reflects the production of bone from the nests.

The assemblages collected below the nests comprised of bone, hair, boluses, eggshell, and feathers. We collected a total of 387 skeletal specimens (NISP-number of individual specimens), including 345 specimens from Nest A and 42 specimens from Nest B. Specimens include complete and incomplete bones, as well as articulated sets of bones. Where possible, the following attributes were noted for each specimen: (1) identity of bone(s); (2) side; (3) taxon; (4) age-sex class; (5) dimensions; (6) association; and (7) damage. Taxonomic assessments were made on the basis of pelage, size, and

morphology of bones and teeth, in comparison with data from museum collections and published sources. For example, colobine femora were sorted from those of guenons and *Lophocebus* by differences in size, degree of projection of the greater trochanter, neck length, and intercondylar breadth (see Nakatsukasa, 1994a,b, 1996).

Age classes of adult, subadult, juvenile, and infant + neonate were based on size, degree of epiphyseal fusion, and tooth eruption. Postcrania were assumed to be from adult animals if epiphyses were completely fused to diaphyses. In bones of adult or nearly adult size, but where epiphyses were cleanly missing or incompletely joined, individuals were assigned to the preadult category. Skulls were considered adult if all molars had erupted or if cranial sutures were closed. Skeletal elements were sexed by size and robustness (see Gautier-Hion, 1975). The soundness of these criteria was confirmed by observations in museum collections of substantial dimorphism in dimensions and extent of muscle markings, particularly in cercopithecoid long bones and scapulae. In adult skulls, tooth size, particularly of canines, was also considered a good indicator of sex.

We calculated the minimum number of elements (MNE) for each element from each taxon and age-sex class. We follow Badgley (1986) and Lyman (1994a) in defining a skeletal element as a single complete bone or tooth. Calculating MNE may become an involved process, especially with large samples or highly-fragmented bones (e.g., Marean et al., 2001). In our assemblage, however, only a small proportion of specimens were fragmented, and there was little question as to whether fragments represented the same or different elements. We calculated minimum number of individuals (MNI; see Grayson, 1984; Klein and Cruz-Urbe, 1984) based on our MNE values.

These values were used to investigate bone survivability and bone fragmentation in the assemblage. We compared bone survivability and fragmentation patterns among all individuals in each primate taxon and *Cephalophus*, in primates versus non-primates, and between preadult and adult primates. To investigate bone survivability, we calculated relative abundances of bones using the formula  $R_i = N_i / (MNI \times E_i)$ , where  $R_i$  is the

relative abundance of a certain element  $i$ ,  $N_i$  is the observed number of a particular element (the MNE value) in the taxon of interest, MNI is the minimum number of individuals in the taxon of interest, and  $E_i$  is the number of skeletal element  $i$  expected in a complete skeleton (see Andrews, 1990; Lyman, 1994b).  $R_i$  values are expressed as a percentage representing bone survivability relative to what would be expected if all skeletons of all individuals had been preserved. It is important to point out, though, that because our MNI values were sometimes summed over different age and sex classes, in many cases no  $R_i$  value approaches 100%.

To investigate bone fragmentation, we looked at the percentage of each element that was whole (unfragmented). For each taxon of interest, we divided the number of whole bones of each element by the NISP to arrive at a value, which we express as a percentage. One hundred percent means that the number of whole elements equals the NISP for that element, and there is no fragmentation.

## Results

### Prey composition

Cercopithecoid monkeys are the predominant prey of crowned hawk-eagles at Ngogo (Table 1). The high percentage of monkeys in the MNI count ( $68/84 = 81\%$ ) closely matches the fraction of monkeys in crowned hawk-eagle kill accumulations from the Kanyawara area of Kibale studied earlier by Skorupa (1989) and Struhsaker and Leakey (1990), 88% and 84%, respectively. Other crowned hawk-eagle prey from Ngogo includes duikers and palm civets, as well as single fruit bats, rodents, and hornbills (Table 1). There are no remains of chimpanzees in the kill accumulations, and no attacks by crowned hawk-eagles on chimpanzees were witnessed in over five years of field research at Ngogo (Mitani et al., 2001). Body mass of the adult mammals in the kill accumulation sample ranges up to around 11 kg (Table 1); perhaps the much larger size of chimpanzee adults (Smith and Jungers, 1997) deters crowned hawk-eagles from predation on chimpanzee infants.

Table 1

Prey assemblage of crowned hawk-eagles at Ngogo, Kibale National Park, Uganda (July 1996–August 1999). Percent values have been rounded to the nearest 0.1%.

Taxon	Adult body mass	NISP	% total NISP	% primate NISP	MNI	% total MNI	% primate MNI
<b>Primates</b>							
<i>Cercopithecus ascanius</i> <sup>a</sup>	4.3 kg (m)	Nest A-165	47.00	53.10	Nest A-22	36.90	45.60
	3.1 kg (f)	Nest B-17			Nest B-9		
<i>Cercopithecus lhoesti</i> <sup>b</sup>	6.0–8.0 kg (m)	Nest A-10	2.60	2.90	Nest A-3	3.60	4.40
	3.0–4.5 kg (f)	Nest B-0			Nest B-0		
<i>Ptilocolobus badius</i> <sup>b</sup>	7.9–10.9 kg (m)	Nest A-21	6.70	7.60	Nest A-6	8.30	10.30
	6.7 kg (f)	Nest B-5			Nest B-1		
<i>Colobus guereza</i> <sup>b</sup>	6.8–11.3 (m)	Nest A-3	0.80	0.90	Nest A-3	3.60	4.40
	5.4–10.9 (f)	Nest B-0			Nest B-0		
<i>Lophocebus albigena</i> <sup>b</sup>	5.7–8.7 (m)	Nest A-10	2.60	2.90	Nest A-2	2.40	2.90
	3.6–8.2 (f)	Nest B-0			Nest B-0		
<i>Papio anubis</i> <sup>c</sup>	(young juvenile, ≈ 3.0–6.0 kg)	Nest A-2	0.50	0.60	Nest A-1	1.20	1.50
		Nest B-0			Nest B-0		
Unidentified cercopithecines		Nest A-93	26.10	29.40	Nest A-17	22.60	27.90
		Nest B-8			Nest B-2		
Unidentified colobines		Nest A-0	2.30	2.60	Nest A-0	2.40	2.90
		Nest B-9			Nest B-2		
<b>TOTAL:</b>		<b>343*</b>	<b>88.60</b>		<b>68</b>	<b>81.00</b>	
Non-primates							
<i>Cephalophus monticola</i> <sup>d</sup>	3.5–9.0 kg	17	4.40		3	3.60	
<i>Nandinia binotata</i> <sup>d</sup>	2.0–3.2 kg	4	1.00		2	2.40	
Megachiroptera		2	0.50		1	1.20	
Rodentia		1	0.30		1	1.20	
Mammalia: Indeterminate		13	3.40		5	6.00	
Aves: Bucerotidae		2	0.50		1	1.20	
Aves: indeterminate		5	1.30		3	3.60	
<b>TOTAL:</b>		<b>44*</b>	<b>11.40</b>		<b>16</b>	<b>19.00</b>	
<b>TOTAL ASSEMBLAGE:</b>		<b>387*</b>			<b>84</b>		

Abbreviations: NISP, number of individual specimens; MNI, minimum number of individuals; m, male; f, female.

<sup>a</sup>Body mass of redbell monkeys at Kibale from Jones and Bush (1988).

<sup>b</sup>Body masses from Delson et al. (2000).

<sup>c</sup>Body mass range for young juvenile baboon based on data for wild baboons in Strum (1991).

\*includes correction for articulations; counting each element (whether articulated or not) as a separate element would lead to NISP values of 413 for primates, 44 for non-primates, and 457 for the whole assemblage.

<sup>d</sup>Body masses from Kingdon (1997).

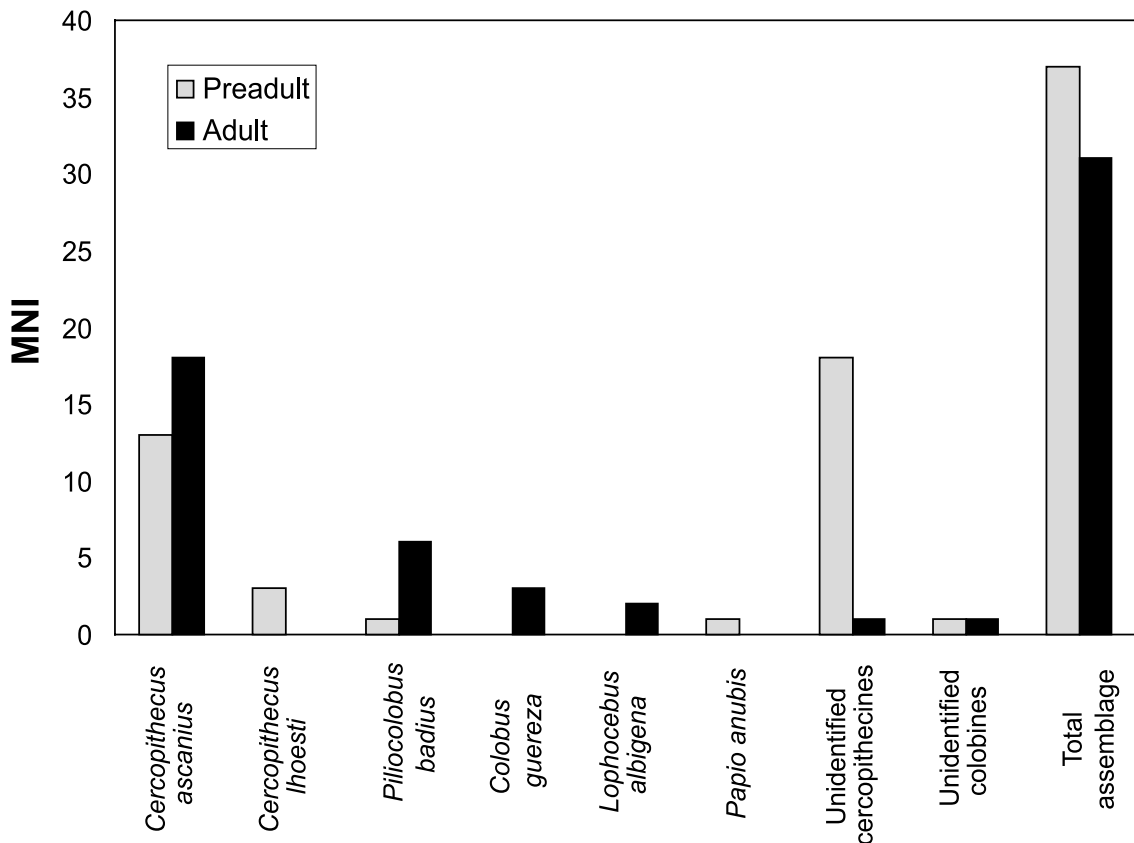


Fig. 1. Minimum number of individuals (MNI) of preadult and adult primate taxa in the Ngogo crowned hawk-eagle kill assemblage.

Of the primate individuals identifiable to species, those attributable to *Cercopithecus ascanius* (redtail monkeys) are by far the most numerous ( $31/47 = 66\%$ ), followed by small numbers of red colobus, black and white colobus, grey-cheeked mangabeys, l'Hoeest's monkeys, and a juvenile olive baboon (Fig. 1). There is no evidence of blue monkeys in the sample. Thirty-one percent of the cercopithecoid sample is too fragmentary and/or too young to identify to species with certainty, but the great majority of these appear to be guenons.

In contrast to the strong selectivity of the Ngogo crowned hawk-eagles for cercopithecoids, and redtail monkeys in particular, they do not show preferences for animals of a particular sex or age-class. Males comprise 55% (16/29) of the portion of the cercopithecoid sample in which sex could be determined, and are over-represented in

the kill sample, since there are more females than males in resident Ngogo monkey populations (Mitani et al., 2001). Adults and preadults are present in approximately expected proportions in the sample (Mitani et al., 2001). Age classes were determined for all cercopithecoid prey individuals (Fig. 1), with adults ( $31/68 = 46\%$ ) and non-adults ( $37/68 = 54\%$ ) nearly equally represented. Although there are more non-adults than adults in cercopithecoid populations at Ngogo, these proportions do not differ from those expected on the basis of chance (Mitani et al., 2001).

#### Bone survivability

For the present crowned hawk-eagle assemblage, there is a clear pattern of bone survivability, dominated by crania and hindlimb bones

(Figs. 2–4). The relatively low bone survivability for most skeletal elements accords with the habit of crowned hawk-eagles to dismember and sometimes cache larger, monkey-sized prey away from the nest (Brown, 1971; Jarvis et al., 1980; Brown et al., 1982; Steyn, 1983; Maisels et al., 1993). This correlates with a feeding preference at the nest for brains and hindlimbs and a tendency to swallow smaller elements whole, which are subsequently digested completely (Brown, 1982; Brown et al., 1982). Often, the trunk is dismembered and its internal organs are consumed at the kill site (Brown, 1971).

Predictably, smaller or more fragile elements such as ribs, vertebrae, tarsals, carpals, phalanges, and metapodials (metacarpals and metatarsals) are poorly represented (Figs. 2–4). Forelimb elements (humerus, radius, ulna) are much less numerous than hindlimb elements (femur, tibia, fibula). Innominate and scapulae are present in inverse proportion to the relative abundance of hind- and forelimb elements in the sample. Similarly, there are fewer mandibles in the sample than anticipated from the relatively good representation of crania and partial crania.

Density-mediated attrition, a potentially important factor in assemblage accumulation (Lyman, 1994c), is unlikely to be responsible for bone survivability and fragmentation patterns at Ngogo. Bone-mineral density values for similar-sized primates and bovids are close enough to one another that the same taphonomic processes would not be expected to produce very different bone survivorship patterns (Pickering and Carlson, 2002). While the patterns of survivorship in primates and *Cephalophus* are similar in the eagle assemblages, the elements that exhibit highest survivability are not those that would be expected based on bone-mineral density values (Pickering and Carlson, 2002).

#### *Damage patterns*

Despite their great strength and impressive killing apparatus, crowned hawk-eagles are fastidious eaters that inflict little damage to bone, compared with mammalian predators (Simons, 1966; Mills and Mills, 1977; Brain, 1981). Of complete crania

in the sample, a high proportion (4/6) are accompanied by their mandibles. Incomplete crania recovered under the nests are usually comprised of calotte pieces and are missing their faces and maxillae. Presumably, when these are removed by the eagles the mandibles are discarded with them, which would account for the much greater number of partial crania ( $n = 47$ ) than isolated dentaries ( $n = 4$ ). Mandibles show minimal breakage; it is significant for comparison with kill assemblages of mammalian predators (e.g., carnivores, chimpanzees) that mandibles in the Ngogo sample commonly retain their rami and angles. Of nine mandibles recovered, just two exhibit damaged rami, each only on one side. Crania of adults are usually intact, but exhibit signs of intense manipulation (Fig. 4). These include talon nicks (small V-shaped holes), punctures (more rounded holes) and “can-opener” perforations (producing bony flaps), often in places convenient for obtaining a good grip, such as orbits (Fig. 5). They are most often found in the orbits, palate, sphenoids, maxillae, and parietals. Diameters of punctures and “can-opener” perforations range from 2–10 mm, and diameters of nicks from 2–4 mm; the majority of these lacerations have a greatest width of 4–6 mm.

In contrast, juvenile monkey crania are usually found torn open basicranially and missing their facial portions (Figs. 4 and 6). Infant crania also typically lack faces, and are disarticulated along their sutures (Figs. 4 and 7a,b). Two associated parietals from an infant redbellied monkey show the effects of the tremendous pressure exerted on the cranium by a crowned hawk-eagle; one also exhibits a “can-opener” perforation made by a talon (Fig. 7b).

There are also distinctive patterns of postcranial damage in the Ngogo crowned hawk-eagle kill sample (Figs. 2–4). There is a clear tendency in the sample for postcranial bones to be minimally broken or unscathed. For example, a high percentage of long bones exhibit no damage, or have had damage limited to the proximal and/or distal ends of the diaphysis (Figs. 8 and 9a). This is true for all size classes of long bones (Fig. 9b). Damage to long bones indicates that crowned hawk-eagles remove the ends by repeated slicing with their



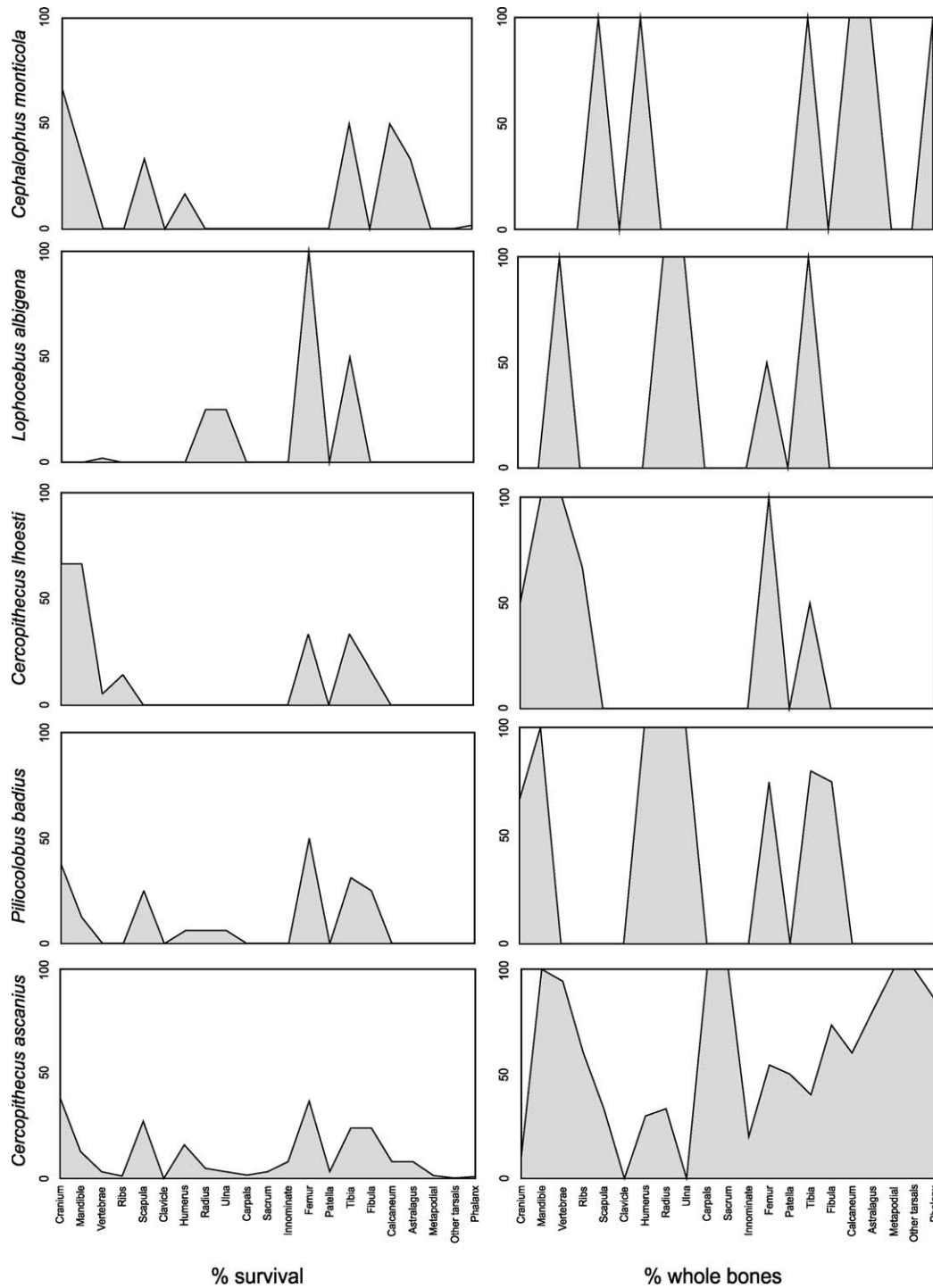


Fig. 2. Bone survivability (percent survivorship, top panels) and fragmentation (percent whole bones, bottom panels) for each primate taxon, as well as the bovid *Cephalophus monticola*, from the Ngogo crowned hawk-eagle assemblage.

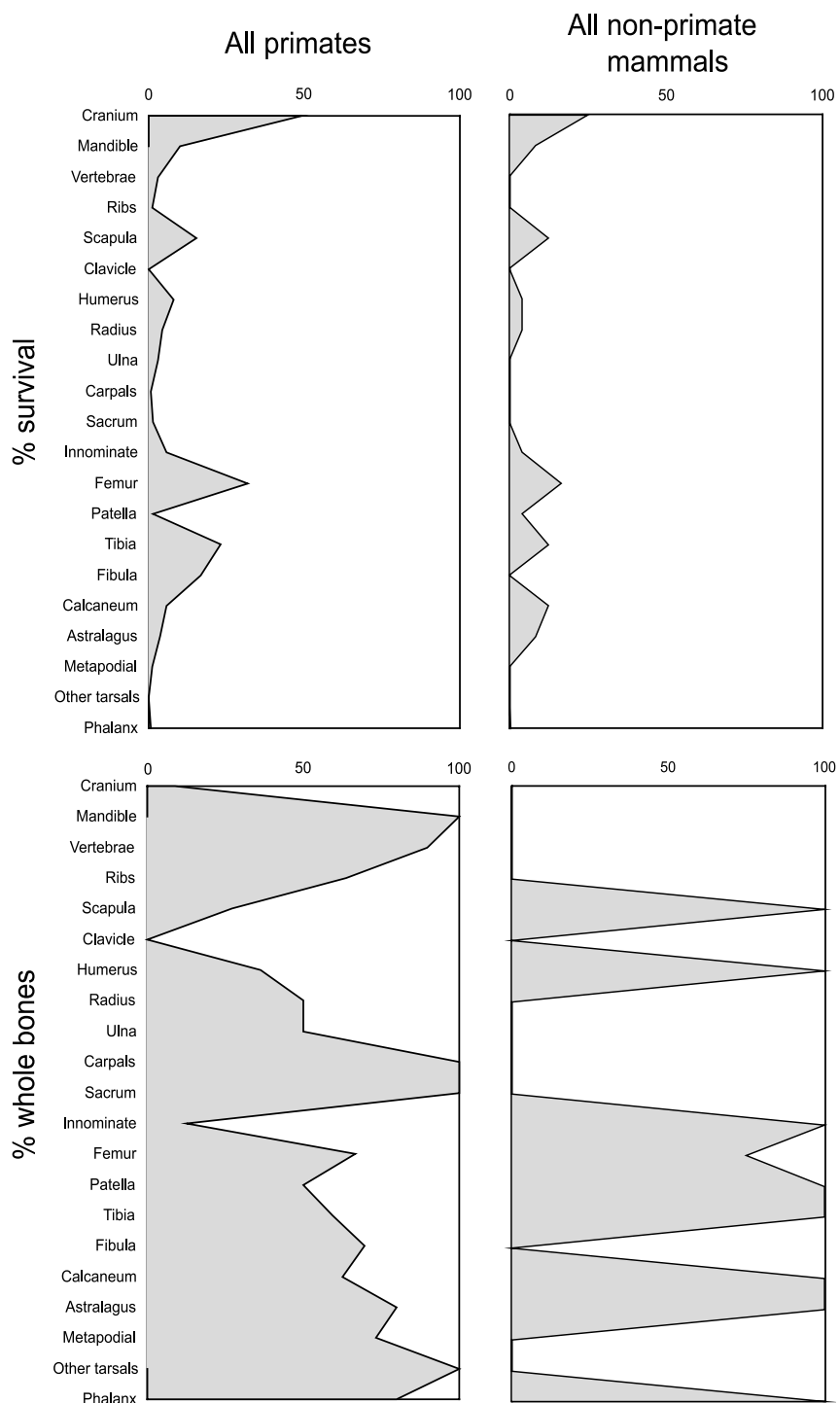


Fig. 3. Bone survivability (percent survivorship, top panels) and fragmentation (percent whole bones, bottom panels) for all primates (left) and all non-primate mammals (right) in the Ngogo crowned hawk-eagle assemblage.



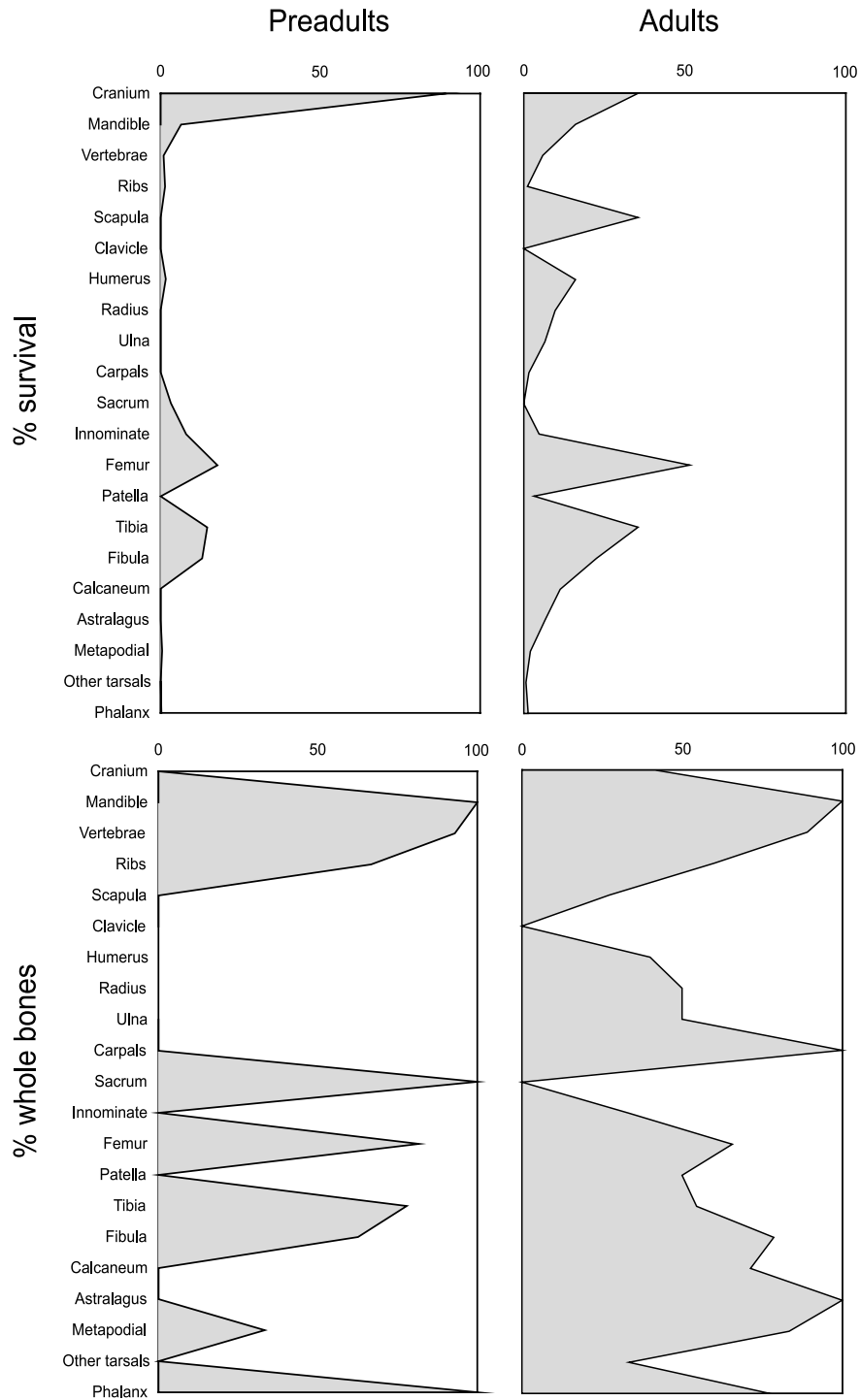


Fig. 4. Bone survivability (percent survivorship, top panels) and fragmentation (percent whole bones, bottom panels) for all preadult (left) and adult (right) primates from the Ngogo crowned hawk-eagle assemblage.

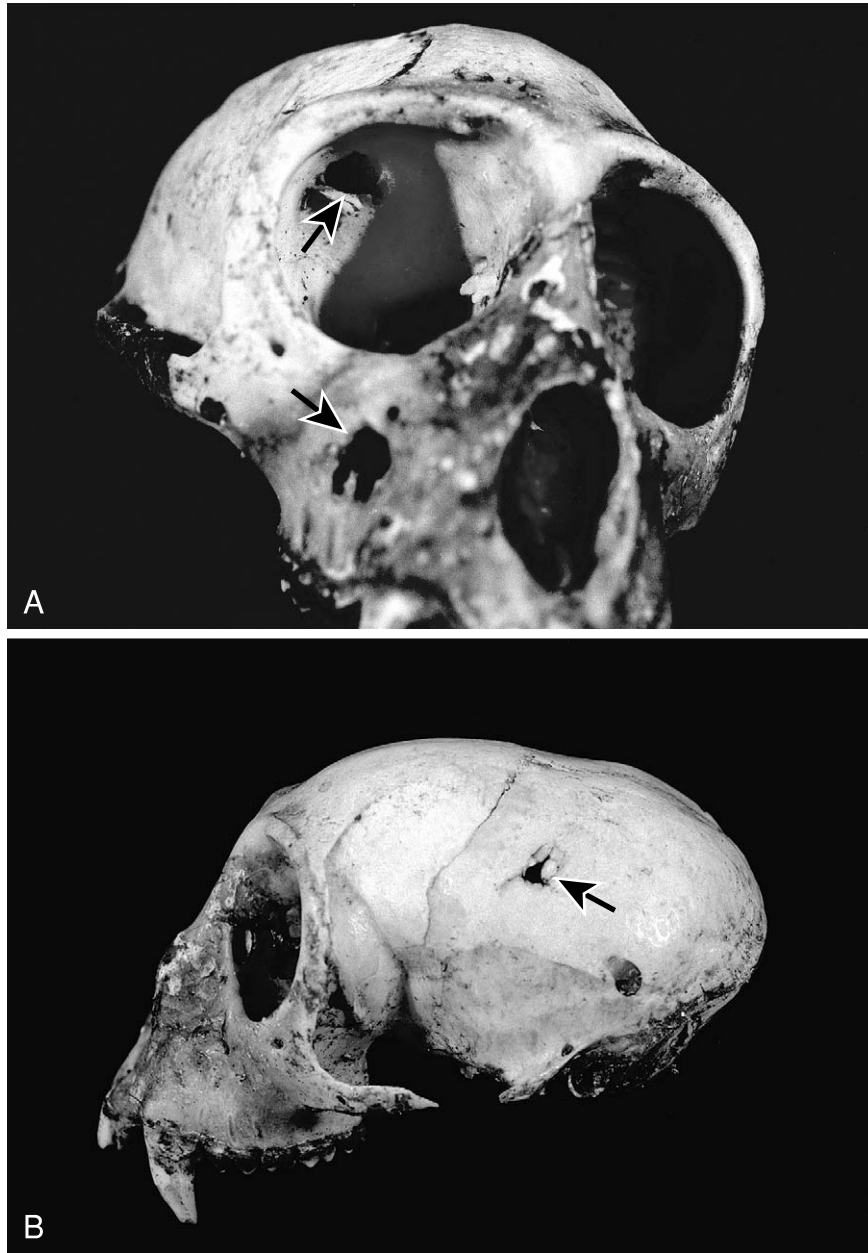


Fig. 5. *Cercopithecus ascanius* cranium from the Ngogo crowned hawk-eagle kill sample. (A) Oblique frontal view. Note talon punctures in orbit and area of infraorbital foramen (arrows). (B) Left lateral view (not to same scale as frontal view). Note perforation in left parietal (arrow) and surrounding bony flaps.

beaks along a narrow circumference. These percentages and the evident concentration of effort to remove ends of long bones near areas of epiphyseal

fusion suggest that crowned hawk-eagles find it difficult to shatter diaphyses to extract marrow. This is supported by the observation that the



Fig. 6. Inferior view, juvenile cercopithecoid crania from the Ngogo crowned hawk-eagle kill sample. The basicranium and face of each have been removed by crowned hawk-eagles.

more robust hindlimb bones are undamaged more frequently (66–76%) than the forelimb elements (54–68%), and have lower incidences of midshaft fracture (hindlimb bones, 11–16% vs. forelimb bones, 17–23%) (Fig. 8).

Most of the remaining postcrania are similarly largely intact, though they may exhibit localized fracturing and “can-opener” perforations from manipulation by talons (Fig. 10). A notable exception is the severe damage inflicted on scapulae (Fig. 11). The blades of these bones are sharply shattered and raked, a consequence of the process of opening the body cavity to extract the heart and lungs (Brown, 1971; Andrews 1990).

## Discussion

Raptors are a major class of predators of anthropoid primates (Fowler and Cope, 1964; Brown, 1971; Rettig, 1978; Seyfarth et al., 1980; Gautier-Hion, 1983; Izor, 1985; Eason, 1989; Skorupa, 1989; Andrews, 1990; Gargett, 1990; Heymann, 1990; Peres, 1990; Struhsaker and Leakey, 1990; Sherman, 1991; Cruz-Urbe and Klein, 1998; Zhang et al., 1998; Zinner and Peláez,

1999; Mitani et al., 2001; Vasquez and Heymann, 2001). One of the most formidable of these is the crowned hawk-eagle, which can kill and lift animals considerably heavier than themselves (Daneel, 1979; Steyn, 1983). In forest habitats where cercopithecoids are common, they are the predominant prey of crowned hawk-eagles (Brown, 1971; Skorupa, 1989; Struhsaker and Leakey, 1990; Mitani et al., 2001). At Ngogo, crowned hawk-eagle predation is sufficiently specialized on redbellied monkeys that it has had a significant negative impact on their local population (Mitani et al., 2001). The correlation between local availability of species and prey selectivity by these eagles helps explain the difference in selection bias at Ngogo for redbellied monkeys and at nearby Kanyawara in Kibale National Park for colobus monkeys (Brown, 1971; Skorupa, 1989; Struhsaker and Leakey, 1990; Mitani et al., 2001). It also accounts for contrasting preferences for monkeys and small antelopes in forests and for hyraxes in more open-country settings (Snelling and Barbour, 1969; Brown, 1971; Steyn, 1973, Tuer and Tuer, 1974; Jarvis et al., 1980; Brown, 1982; Brown et al., 1982; Steyn, 1983; Tarboton and Allen, 1984; Cruz-Urbe and Klein, 1998). Where prey

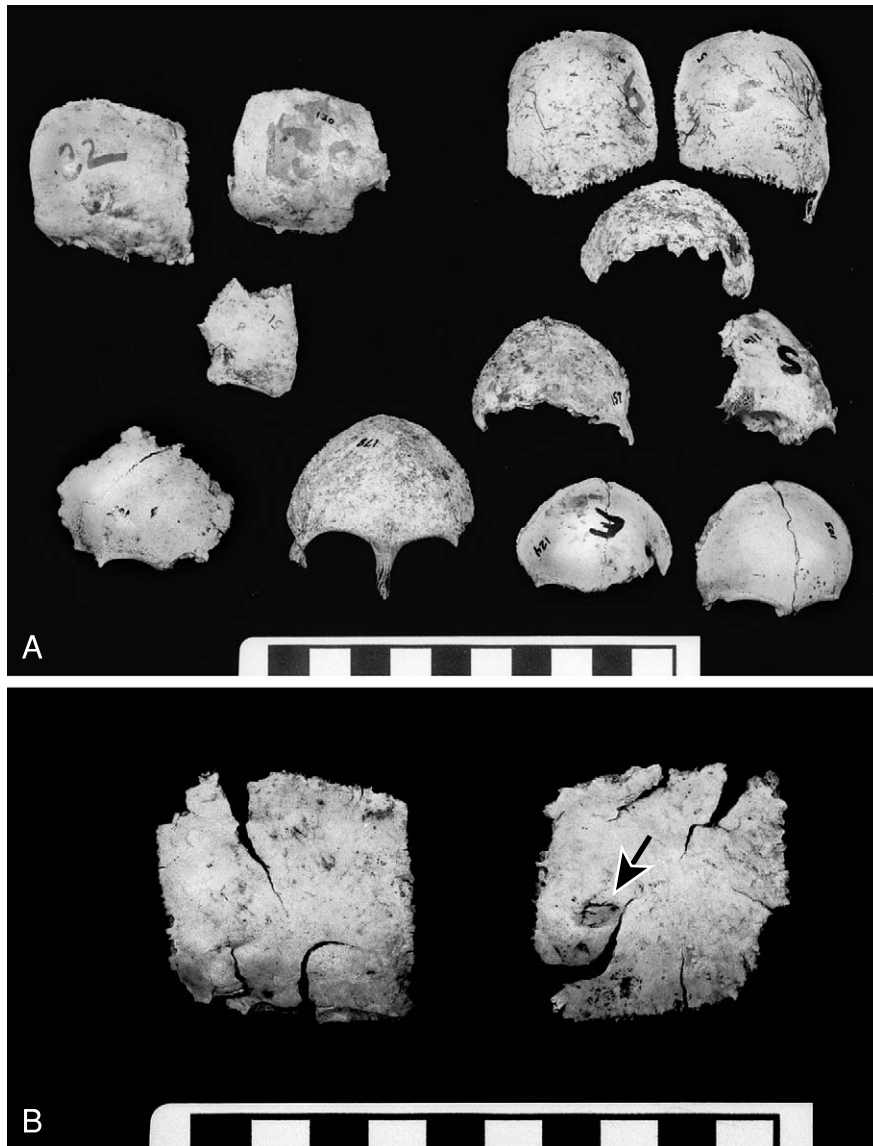


Fig. 7. Cranial bones of infant cercopithecoids dismembered by crowned hawk-eagles at Ngogo. (A) Parietals and frontals. (B) Left and right parietal bones of a guenon. Note the patent sutures, cracking due to compression, and the “can-opener” talon puncture (arrow).

accumulations have been quantified, it appears that crowned hawk-eagles narrowly concentrate on one or several prey species (Tuer and Tuer, 1974; Jarvis et al., 1980; Brown, 1982; Brown et al., 1982; Steyn, 1983; Tarboton and Allen, 1984; Skorupa, 1989; Struhsaker and Leakey, 1990; Cruz-Uribe and Klein, 1998; Mitani et al., 2001).

Although it is possible that feeding behavior and ability to fully digest small bones obscures the contribution of small animals to their kill aggregations (Jarvis et al., 1980; Brown, 1982), the recovery from below Nests A and B of tiny skeletal elements from a number of small mammals suggests that the range of taxa in the Ngogo kill

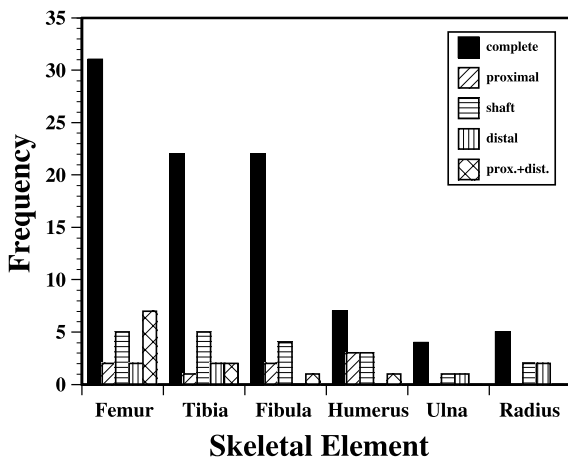


Fig. 8. Incidence of damage to long bones in the Ngogo crowned hawk-eagle kill sample. Tallies are recorded of bones with no damage ("complete"), with damage only to the proximal ("proximal") or distal ("distal") end, with damage to both proximal and distal ends ("prox. + dist."), and of bones with mid-shaft breakage ("shaft").

sample is adequately represented. By comparison, the eclectic prey lists from kill accumulations of crowned hawk-eagles compiled by Jarvis et al. (1980) are partly artifacts of being composites of observations from many nests; even so, 77% of the largest composite sample is composed of just three taxa (hyrax and two species of bovid). In this regard, crowned hawk-eagles differ from other raptors (e.g., fish eagles, owls), which show a wider prey selectivity (see, for example, Andrews, 1990; Stewart et al., 1997, 1999).

The bone survivability profile of the kill sample of the Ngogo crowned hawk-eagles is also distinctive. Tendencies to dismember and cache animals away from the nest and to feed on particular parts of the carcass at the nest contribute to low relative abundances of individual elements. Crania, hindlimbs, and scapulae are the most commonly represented elements in bone accumulations below the nests of crowned hawk-eagles at Ngogo and apparently elsewhere (cf. Brown, 1982). There are also clear patterns of bone damage in these aggregations. Long bones tend to be complete or deliberately opened at their ends. Scapular blades are heavily damaged and raked. Adult (and subadult) crania show numerous nicks, punctures, and

"can-opener" perforations, but are usually otherwise complete and accompanied by their mandibles. Juvenile crania have their faces and basicrania removed; infant and neonate crania also have their faces broken away, but are usually disarticulated along their sutures and are represented by whole bones (e.g., parietals, occipital). This is surprising given the power of crowned hawk-eagle talons and the fragility of infant and neonate cercopithecoid cranial bones. If the type and frequency of damage to individual bones and bone survivability patterns in the Ngogo sample prove consistent with observations on samples from other sites, they will provide a reliable basis for recognizing the effects of crowned hawk-eagle predation in fossil assemblages.

To date, the most direct and provocative paleo-anthropological implication of crowned hawk-eagle predation is Berger and Clarke's (1995) hypothesis that this or a similar large raptor may have been primarily responsible for the accumulation of fauna at the late Pliocene site of Taung, South Africa, including the infant type specimen of *Australopithecus africanus*. Results of our study generally support an interpretation of some contribution by large raptors to the Taung fossil assemblage. For instance, as in the Ngogo crowned hawk-eagle kill sample, the Taung fauna contains a preponderance (85%) of small-to-medium-sized animals; it includes a good representation of cercopithecoid (small baboon) fossil bones and crania; it preserves numerous complete or nearly complete mammalian crania in association with mandibles, including that of the Taung child at the time of deposition; many of the long bones from the Taung fauna are largely complete; and puncture marks on skulls from Taung exhibit V-shaped nicks, "can-opener" flaps, and compression cracks, but not the more severe damage characteristic of mammalian predators (see Brain, 1981).

There are, however, clear differences between the kill accumulation from Ngogo and the Taung sample. The ample presence of hyrax fossils and the predominance of baboons suggests that the Taung fauna derived from more open conditions than the prey aggregation from Ngogo, but this does not preclude eagle involvement. More importantly, the upper size range of mammalian taxa at





Taung, which includes leopards and buffaloes (Cook, 1990; McKee, 1993a,b; Berger and Clarke, 1995), probably exceeds the hunting capabilities of eagles, indicating that other agencies of accumulation were responsible as well. At the other end of the size spectrum, the association of diverse small mammals, eggshells, and crab carapaces at Taung suggested to Brain (1981) the activity of other birds, such as eagle owls.

The Taung fauna is also mixed in another way. While considered by Cooke (1990: p. 122; but see McKee, 1993a) to represent “a coherent whole . . . essentially from a single fairly short phase of deposition,” it is actually a composite of fossil material from several localities (e.g., “Dart deposits” and “Hrdlicka deposits”; McKee, 1994), making it even less likely to have been amassed by a single animal or type of animal. Indeed, most of what is known about the overall character of the Taung fossil assemblage is based on taxa from the Hrdlicka deposits and not from the more faunally depauperate hominid type site (McKee, 1994).

The likelihood of faunal mixing and multiple accumulating agents makes it difficult to evaluate rigorously the possibility of eagle involvement in the death of the Taung child. Furthermore, there is no evidence of crowned hawk-eagles or other raptors attempting to take infant chimpanzees, which are similar in size to the estimated body mass of 10–12 kg for the Taung child (Berger and Clarke, 1995), at Ngogo or elsewhere (Mitani et al., 2001). Nevertheless, a crowned hawk-eagle was observed to attack a human child, and in one instance an infant human cranium was discovered in a crowned hawk-eagle nest (Steyn, 1983). Although no young primate killed by crowned hawk-eagles at Ngogo is larger than a juvenile baboon, these cases and the size range of crowned hawk-eagle prey suggest that it is reasonable to believe that they were capable of killing an infant australopithecine. Despite the fact that infant primate skulls in the Ngogo sample are all disarticu-

lated, the cranium of the Taung child is much larger and more thickly-walled, and therefore would have been more capable of resisting such disintegration, in the manner of a skull from an adult cercopithecoid. In addition to its completeness, the association of a cranium of that size with its mandible seems more typical of eagle prey remains than those of mammalian predators. Finally, the puncture and surrounding depressed fracture in the cranium of the Taung child, preserved now as features on the endocast, are consistent with the type of damage observed on bone in the Ngogo sample. Thus, while the Taung fauna appears to represent a mix of deposits and the behavior of multiple predators, the involvement of a large raptor like the crowned hawk-eagle in the death of the Taung child cannot be ruled out. Because Berger and Clarke (1995) did not quantify skeletal damage and bone survivability patterns, however, the taphonomic impact of a predator such as the crowned hawk-eagle in the Taung faunal assemblage remains unclear. Further assessment of their hypothesis will require a more comprehensive examination of the faunal collection from the hominid type site at Taung.

## Summary

Taphonomic analysis of a prey assemblage of crowned hawk-eagles from the Ngogo study area in Kibale National Park, Uganda revealed distinct patterns of prey selection, bone damage, and survivability of skeletal elements. The animals in the prey assemblage are small-to-medium-sized, ranging up to about 11 kg in body mass, and are predominantly cercopithecoid monkeys (81%). Redtail monkeys are particularly well represented in this faunal accumulation, composing 66% of the cercopithecoid monkeys identifiable to species. This strong prey selectivity may reflect the contribution that monkeys make to the mammalian

Fig. 9. (A) Cercopithecoid long bones from the Ngogo crowned hawk-eagle kill sample with proximal and distal ends removed for the extraction of marrow. (B) Cercopithecoid femora from the Ngogo crowned hawk-eagle kill sample. From left to right, two neonate femora, and adult femora of *Cercopithecus ascanius* (female and male individuals), *Cercopithecus lhoesti*, *Colobus guereza*, *Piliocolobus badius*, and *Lophocebus albigena*.



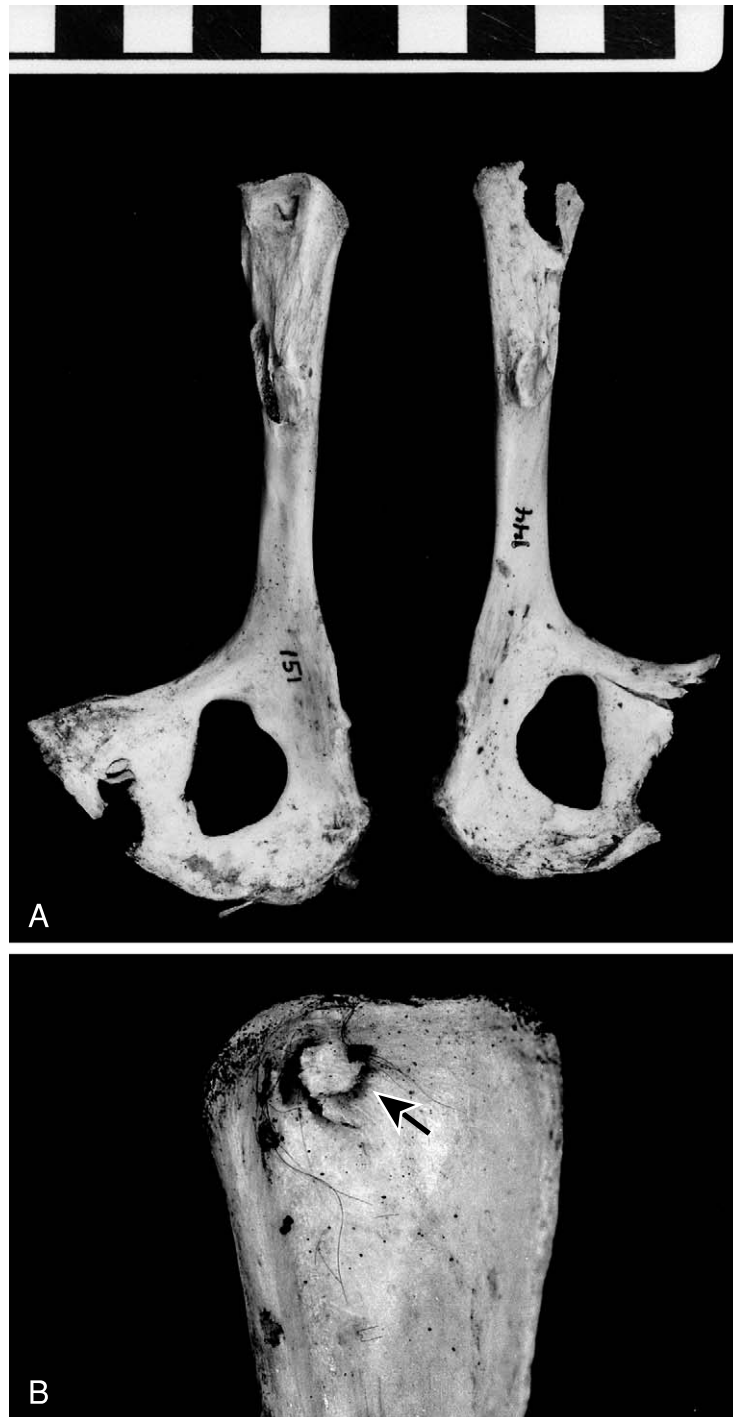


Fig. 10. Cercopithecoid innominates from the Ngogo crowned hawk-eagle kill sample. (A) Left and right innominates, *Cercopithecus ascanius*. Note the talon damage to the ilia and pubic areas. (B) Enlarged detail of a “can-opener” perforation (arrow) through the ilium of the right innominate (#151), lateral view.



Fig. 11. *Cercopithecus ascanius* scapulae from the Ngogo crowned hawk-eagle kill sample. Note the damage caused by raking and perforation with talons.

biomass in the Ngogo area, and the local availability of species. Conversely, the Ngogo kill sample shows little or no sign of preference for animals of a particular sex or age-class.

In addition to an evident concentration on particular taxa, the Ngogo kill sample also exhibits conspicuous features of bone survival and damage, including: (1) better representation of crania, hind-limb elements, and scapulae than other elements; (2) tendency for adult crania to remain complete and to be accompanied by their mandibles; (3) faces and basicrania are destroyed, and mandibles dissociated from crania in young individuals; (4) mandibles are largely undamaged; (5) long bones tend to be complete or opened only at their ends; (6) thin bones, such as crania and innominates, exhibit numerous nicks, punctures, and “can-opener” perforations; and (7) scapular blades are heavily damaged and raked. If these features are consistent for crowned hawk-eagle kill assemblages, they may prove useful for recognizing the

taphonomic signature of such large raptors in fossil assemblages. Indeed, comparison of information on the fossil fauna from the late Pliocene site of Taung, South Africa with the results of our analysis indicates that crowned hawk-eagles or a similar large raptor had a role in the accumulation of that fauna, including the infant type skull of *Australopithecus africanus*. Future study of the Taung fauna in a manner similar to our analysis of the Ngogo kill sample is necessary for a more rigorous evaluation of the extent of contribution of large raptors to the fossil deposit from the hominid type site and the probability that such a predator killed the Taung child.

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