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Infanticide in Chimpanzees: Taphonomic Case Studies from Gombe

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Abstract

Objectives

We present a study of skeletal damage to four chimpanzee (*Pan troglodytes*) infanticide victims from Gombe National Park, Tanzania. Skeletal analysis may provide insight into the adaptive significance of infanticide by examining whether nutritional benefits sufficiently explain infanticidal behavior. The nutritional hypothesis would be supported if bone survivorship rates and skeletal damage patterns are comparable to those of monkey prey. If not, other explanations, such as the resource competition hypothesis, should be considered.

Methods

Taphonomic assessment of two chimpanzee infants included description of breakage and surface modification, data on MNE, %MNE, and bone survivorship. Two additional infants were assessed qualitatively. The data were compared to published information on monkey prey. We also undertook a review of published infanticide cases.

Results

The cases were intercommunity infanticides (one male and three female infants) committed by males. Attackers partially consumed two of the victims. Damage to all four infants included puncture marks and compression

fractures to the cranium, crenulated breaks to long bones, and incipient fractures on ribs. Compared to monkey prey, the chimpanzee infants had an abundance of vertebrae and hand/foot bones.

Conclusions

The cases described here suggest that chimpanzees may not always completely consume infanticide victims, while reports on chimpanzee predation indicated that complete consumption of monkey prey usually occurred. Infanticidal chimpanzees undoubtedly gain nutritional benefits when they consume dead infants, but this benefit may not sufficiently explain infanticide in this species. Continued study of infanticidal and hunting behavior, including skeletal analysis, is likely to be of interest.

1 INTRODUCTION

Chimpanzees (*Pan troglodytes*) hunt and consume vertebrate prey at most long-term study sites, and red colobus monkeys (*Procolobus* spp.) are the most commonly hunted prey (Boesch, 1994; Mitani & Watts, 2001; Newton-Fisher, 2007; Stanford, 1998; Stanford, Wallis, Matama & Goodall, 1994a). Like many other mammals (Lukas & Huchard, 2014), chimpanzees sometimes commit infanticide. Such killings occur infrequently, but have been observed at most long-term study sites (Wilson et al., 2014). Infanticide accounts for a substantial portion of infant mortality (e.g., Nishida et al., 2003; Williams et al., 2008). Chimpanzees sometimes consume infanticide victims, much like monkey prey (e.g., Suzuki, 1971).

While the sexual selection hypothesis (Hrdy, 1979) explains why infanticide occurs in most primate species, it does not entirely explain chimpanzee infanticide (Palombit, 2012; van Schaik, 2000). The resource competition hypothesis proposes that killing the infant of a conspecific reduces future competition for resources and/or mates for the infanticidal animals and their offspring. Chimpanzee infanticide matches predictions from the resource competition hypothesis in that between-group infanticides decrease a neighboring community's future coalition strength and, along with other forms of intergroup aggression, expand the territory of the infanticidal males (Kutsukake & Matsusaka, 2002; Mitani, Watts, & Amsler, 2010; Newton-Fisher, 1999; Sherrow & Amsler, 2007). Territory expansion in chimpanzees can improve access to food resources as well as increase access to females for the males (Goodall, 1986; Sherrow & Amsler, 2007; Watts, Mitani, & Sherrow, 2002; Williams, Oehlert, Carlis, & Pusey, 2004). Within-group infanticide, particularly instances perpetrated by adult females (Goodall, 1977; Mitani et al., 2010), may also be a resource competition strategy, in which females seek to eliminate feeding competitors (Hrdy, 1981; Pusey, 1983) and to deter other females from using their foraging range (Goodall, 1986; Hiraiwa-Hasegawa & Hasegawa, 1994; Pusey et al., 2008).

Because chimpanzee infanticide victims are sometimes entirely (including skeletal elements) or partially consumed (see Table 3), the exploitation hypothesis for infanticide cannot be ignored. The exploitation hypothesis likely applies to many species, with conspecifics consuming the unguarded young of others (Fox, 1975). It is rarely invoked in studies of primates, however. The costs of obtaining an infant for purely nutritional reasons are likely high in primates compared to many other species, because mothers carry and defend their infants. Nonetheless, in species such as chimpanzees and baboons (*Papio* spp.), which prey on the young of other primate species (Stanford, 1998; Strum, 1983), unrelated individuals of their own species may also represent a tempting package of tender, nutrient-dense meat. The widespread consumption of infanticide victims in chimpanzees suggests that this hypothesis should be considered (Murray, Wroblewski, & Pusey, 2007).

We examine whether the nutritional hypothesis provides sufficient explanation for chimpanzee infanticide through a review of published infanticide cases as well as a taphonomic study of skeletal damage to infanticide victims. The resource competition hypothesis will be further supported if nutritional benefits alone do not explain chimpanzee infanticide.

The exploitation hypothesis predicts that attackers commit infanticide to obtain nutritional benefits. If this is the case, attackers should therefore consume their victims entirely, or at least as intensively as they consume monkey prey. We tested this prediction using two sets of data: (a) behavioral observations, including published accounts and one new case; and (b) examination of the skeletal remains of four infanticide victims, with comparison of the damage to the chimpanzee infants' bones versus published data on damage to bones of monkey prey (Plummer & Stanford, 2000; Pobiner, DeSilva, Sanders, & Mitani, 2007).

Behavioral similarities between hunting and infanticide include the most common method of capture, being snatched from the mother (Stanford et al., 1994a; Stanford, Wallis, Mpongo, & Goodall, 1994b; Takahata, Hasegawa, & Nishida, 1984), and the common kill method, biting the head or abdomen (Arcadi & Wrangham, 1999; Kawanaka, 1982; Stanford et al., 1994b; Takahata et al., 1984; Teleki, 1973; Watts et al., 2002). The methods of consumption and order of consumption (when applicable) are also similar between infanticide and monkey hunting, in that pieces of flesh are usually removed with the teeth and hands, begging and some meat sharing may occur, and the extremities or abdomen are consumed first (Hamai, Nishida, Takasaki, & Turner, 1992; Kawanaka, 1982; Nishida, Uehara, & Nyondo, 1979; Takahata et al., 1984; Teleki, 1973). During the capture and consumption of monkeys and other prey, Kawanaka noted that the participating chimpanzees "repeatedly cried out, and it was apparent that they were all unusually excited" (Kawanaka, 1982, p. 367). Excitement signs include screaming and other vocalizations, piloerection, display behavior, and high speed movements (Goodall, 1986; Stanford, 1998; Teleki, 1973). Published reports noted similar behaviors in some infanticide incidents, and several previous studies drew attention to the similarities between hunting and infanticidal attacks (Hamai et al., 1992; Sherrow & Amsler, 2007). By comparing skeletal damage to chimpanzee infanticide victims versus monkey prey, we seek to clarify whether conspecific infants were likely killed primarily for food, or for some other reason.

For both hunting and infanticide, observers have sometimes indicated that if either monkey prey or chimpanzee infanticide victims are consumed, they are entirely consumed, with only small fragments, such as a piece of pelt, remaining (e.g., Takahata et al., 1984; Teleki, 1973). Chimpanzees at least sometimes ingest bones from their prey, particularly from the hands and feet (Tappen & Wrangham, 2000). Nutritional benefits of these two behaviors may be sufficiently comparable (see discussion on body size in Methods section), but it is more difficult to determine whether hunger or some other motivation helps drive either behavior. At Gombe, monkey hunting is more common when fruit is plentiful (Stanford, 1998; Stanford et al., 1994a, 1994b), while infanticide does not seem to have seasonality. It is also challenging to determine degree of consumption from published descriptions of either hunting or infanticide. This may be due to the difficulty of observing a consumption episode in sufficient detail. We therefore turn to skeletal evidence to further test the validity of the nutritional hypothesis for chimpanzee infanticide.

If the nutritional hypothesis provides sufficient explanation for chimpanzee infanticide, we expect the following predictions to be true: (a) types of skeletal damage (e.g., break type) between chimpanzee infanticides and monkey prey will be similar, (b) bone fragmentation (NISP/MNE) will be similar between the two samples, (c) skeletal element representation (bone survivorship: observed/expected MNE) will be similar between the two samples, and (d) published descriptions of infanticides will indicate that the victim was thoroughly consumed in nearly all cases, as in reports on monkey hunting.

2 MATERIALS AND METHODS

2.1 Study site and population

We analyzed behavioral data and skeletons collected during the course of the long-term study of chimpanzees at Gombe National Park, Tanzania. Gombe is located in northwestern Tanzania on the shore of Lake Tanganyika, and covers approximately 35 km^2 (Pusey, Pintea, Wilson, Kamenya, & Goodall, 2007). There are currently three communities of chimpanzees at Gombe: the central Kasekela Community, studied since 1960 (Goodall, 1986), the northern Mitumba Community, which began to be habituated and observed in 1985 (Pusey et al., 2007), and

the southern Kalande Community, which has been monitored since 1999 but remains unhabituated (Rudicell et al., 2010). In Kasekela and Mitumba, a team of two Tanzanian field assistants follows a single focal chimpanzee all day, from before dawn to after dusk, if possible. Chimpanzees sleep in simple nest platforms in trees, and field assistants attempt to follow each focal target from when it leaves its nest in the morning until it builds a new nest in the evening. Observers record data on map location and party composition every 15 min, maintain a continuous record of the focal target's feeding, grooming, mating and aggressive behavior, and record *ad libitum* narrative notes on behaviors such as tool use and intergroup encounters (Goodall, 1986; Pusey et al., 2007; Wilson, 2012).

At Gombe, the bodies of dead chimpanzees are recovered whenever possible for necropsy and soft tissue pathology assessment, as well as skeletal preservation and study (Terio et al., 2011). After necropsy, chimpanzees are buried in permeable bags for at least 1 year before exhumation during the dry season. Chimpanzees are buried in permeable bags to help ensure complete recovery of all skeletal elements. After exhumation, skeletons are carefully cleaned in water with a soft brush, left to dry thoroughly, inventoried, and stored in mosquito net bags to help guard against insects.

2.2 Behavioral observations

To assess the degree of consumption recorded during behavioral observations of infanticide, we examined published accounts of infanticidal attacks, and one new observation, and listed demographic information about the infant, sex of the attackers, whether the infanticide was an inter- or intracommunity event, and whether the infant was consumed. We characterized extent of consumption into six categories (Table 1). Complete consumption here means the ingestion of all body cavity contents, flesh from the limbs, as well as ingestion of at least some skeletal material. We employed this definition of complete consumption because monkey prey consumption was often described in this way, particularly at Gombe (Goodall, 1986; Teleki, 1973), where "normally every scrap of bone, meat, and hair is consumed" from red colobus prey (Stanford, 1998, p. 64).

Table 1. Categories of degree of consumption

Degree of consumption	Definition
Partial consumption, voluntary abandonment	Observers indicated that the carcass was abandoned at some point after consumption had begun.
Partial consumption, forced abandonment	Observers indicated that the carcass was abandoned at some point after consumption had begun, and the abandonment was a direct result of intervention by the infant's mother, natal community, or some other external force.
Complete consumption, including at least some skeletal elements	Observers recorded that the carcass was entirely consumed, including at least some skeletal elements. This category does not include cases where body cavities were left intact or only partially consumed.
Partial consumption, but degree uncertain.	Observers could not determine or did not record extent of consumption, but did indicate that at least some consumption of the carcass occurred.
Not consumed, voluntary abandonment	Observers indicated that the carcass was abandoned without being consumed. This category includes cases where the infant was abandoned while still alive and subsequently died. No interventions by the infant's mother, natal community, or other external forces were recorded.
Not consumed, no opportunity for consumption	Observers indicated that the infant's mother or other natal community members retained or reclaimed infant, either before or after time of death, thus providing

Degree of consumption	Definition
	no opportunity for the killers to consume. Chimpanzees who reclaimed the infant also did not consume it.
Uncertain.	Observers were not able to observe events following an infanticide.

2.3 Skeletal analysis

We examined the skeletons of four chimpanzee infanticide victims housed by the Gombe Stream Research Center. We have summarized details of the circumstances of each death below (see Results section). Due to logistical constraints, we only collected data on gross damage to the skeletons of two infants killed in 1975 (Goodall, 1977). One of us (CAK) briefly examined these two skeletons (Case 1 and Case 2) in 2008. We therefore assessed skeletal damage for these two cases qualitatively. The other two infants, Rejea and Andromeda, were killed in 1993 and 2005, respectively (Wilson, Wallauer, & Pusey, 2004; Terio et al., 2011). One of us (CAK) examined these skeletons in detail in 2009 and identified the remains by skeletal element, examined each element under diffuse light for surface modification using a 10× hand lens, and recorded antemortem and perimortem skeletal traumata. For these two infants, we also recorded the number of bone specimens identifiable to element and taxon (Number of Identified Specimens, or NISP) and the minimum number of complete skeletal elements represented by the assemblage (Minimum Number of Elements, or MNE), which includes both partial and complete bones. For each measure (NISP and MNE), we calculated percentages of (%)NISP and (%)MNE: this is the percentage of the assemblage made up of a particular element. For example, Rejea's skeleton includes a total of 164 identified specimens (NISP), and 25 of these are cranial fragments; the %NISP for the cranium is 16% (see Results section for complete data). To facilitate direct comparison, skeletal modifications were defined in the same way as Pobiner et al. (2007, Table 3). We also calculated bone survivorship (observed/expected MNE) and bone fragmentation (NISP/MNE), after Pobiner et al. (2007), for each infant separately as well as for Andromeda and Rejea together. Expected MNEs for the chimpanzee infants are based on modal numbers of vertebrae (seven cervical, 13 thoracic, four lumbar, and six sacral) from Schultz and Straus Jr. (1945) and ossification data from Schultz (1940) and Winkler (1996). We expected that chimpanzee infants 3–9 months old would have 20 metapodials (metacarpals and metatarsals, term used by Pobiner et al., 2007), and 20 carpals/tarsals (Nissen & Riesen, 1949; Winkler, 1996). We combined carpals and tarsals into a single category because there are no carpals in the red colobus prey sample (Pobiner et al., 2007) and to facilitate identification of skeletal elements that were not fully formed. While comparisons focused on the red colobus prey sample from Kibale National Park, Uganda, analyzed by Pobiner and colleagues (2007), we also contrasted the chimpanzee infanticide victims with a red colobus prey sample from Gombe analyzed by Plummer and Stanford (2000).

The absence of any healing of the traumata described in these infanticide cases suggests that the skeletal damage occurred around the time of death [antemortem skeletal injuries would exhibit reactive bone/calluses, depending on the time elapsed since the injury (Buikstra & Ubelaker, 1994; Galloway, Zephro, & Wedel, 2014b)]. Postmortem damage/diagenic change was distinguished from perimortem trauma based on accepted morphological characteristics (Pobiner et al., 2007, Table 3). Fracture types were identified using the criteria outlined by Pobiner and colleagues (2007), with "crenulated edges" comprising frayed and ragged edges at the ends of long bones, "step fractures" resulting from static loading creating a stair-step appearance of fractures, "compression fractures" resulting from approximately equal and opposite loads affecting two sides of an element, and "incipient fractures" referring to breaks that pass through only a portion of a bone (rather than its entire diameter) (Pobiner et al., 2007; Zephro & Galloway, 2014). This fracture type is also called an "incomplete fracture" (Galloway, Zephro, & Wedel, 2014a), but we retained the same nomenclature used by Pobiner and colleagues (2007).

We present quantitative data on Andromeda and Rejea separately because while Rejea was partially consumed, Andromeda was not. We also present combined data for both these infants as a point of comparison since chimpanzee infanticide victims are not always consumed, even when it is possible for the killers to do so (see Table 3). This has the potential to provide information on skeletal damage caused by consumption versus killing.

Monkey prey provide an appropriate comparison for infanticide victims both because these two categories of animals are approximately the same size (nutritional value is therefore presumably comparable), and also because behavioral similarities between monkey hunting and chimpanzee infanticide have been noted in published accounts. These similarities include behavior preceding and during the hunt/infanticide, capture method, kill method, and consumption order (when applicable) (e.g., Hamai et al., 1992; Sherrow & Amsler, 2007). Adult red colobus at Gombe weighed an average of 10.5–11 kg for males and 7–7.5 kg for females (Struhsaker, 2010). Neonate red colobus were estimated to weigh 0.5–0.75 kg, with older infants massing approximately 1–4 kg, and juveniles 2–4 kg (Stanford, 1998). At most study sites, immature red colobus were preferred prey relative to adults (Nishida et al., 1979; Pobiner et al., 2007; Stanford, 1998; Stanford et al., 1994a; Watts & Mitani, 2002), and at Gombe the mean prey weight was 4.4 kg (Stanford, 1998). Chimpanzees averaged 1.7–1.8 kg at birth (in captivity) (Fessler, Navarrete, Hopkins, & Izard, 2005; Gavan, 1971), and ranged between 0.67 and 3.3 kg at birth (Fessler et al., 2005). The infanticide victims examined here range from 3 to 9 months of age, and chimpanzees of this age generally seem to be close to the mean prey weight for Gombe. The mean body mass for captive 3-month-old chimpanzees was approximately 3 kg (range 1.5–3.5 kg), while the mean body mass for 9-month-old chimpanzees is 4.5 kg (range 2–5 kg) (Marzke et al., 1996), though another captive infant was recorded to weigh 9.5 kg at 9 months (Vančata & Vančatová, 2002). While captive chimpanzees tend to be larger than their wild counterparts (Zihlman, Bolter, & Boesch, 2007), and chimpanzees at Gombe are significantly smaller in terms of both body length and mass than other chimpanzee populations (Pusey, Oehlert, Williams, & Goodall, 2005), infant chimpanzees are approximately the same mass as sub-adult red colobus, and may approach the mass of adult red colobus. Certainly they are the same size class as red colobus of any age (size class 1, per Brain, 1981). While differences in skeletal maturity prevent some comparisons (discussed below), describing types of skeletal damage and examining bone survivorship remain potentially valuable contrasts between chimpanzee infanticide victims and red colobus prey, particularly because the red colobus prey sample is dominated by sub-adult monkeys (Pobiner et al., 2007).

In addition to sample size, further limitations of this study include indicators from the behavioral record that infanticide and monkey hunting behaviors differ in significant ways (e.g., in treatment of the carcass as described in Goodall 1977 and elsewhere). Motivations for these two behaviors may not be exactly the same. Another limitation is contrasting skeletal damage patterns created by different groups of chimpanzees (monkey prey sample from Kibale, but infanticide victims from Gombe). Additional comparisons across different populations of chimpanzees may be possible in future.

3 RESULTS

3.1 Brief descriptions of the infanticide cases

3.1.1 Case 1: 1975 male

Here, we provide a brief summary; see Goodall (1977) for the full description. According to the original publication, this event occurred in October 1975 (Goodall, 1977), but on examining the long-term records, we found that it occurred on 30 September, 1975 (GSRC Data). The observer estimated the infant to be 1.5–2 years old at death (Goodall, 1977), but because of comparison of skeletal and dental maturation to a chimpanzee infant of known age (Andromeda), we estimated the age to be closer to 9 months (Kirchhoff, 2010). The killing was not directly observed, but, due to the types of calls heard (chimpanzees fighting rather than alarm calls indicating another predator) and that blood still flowed from the infant's wounds, field assistant Bambanganya inferred that the adult male chimpanzees had killed the infant approximately 15 min earlier. The carcass was partially consumed and used in displays. A young female also sniffed at and then groomed the carcass. The

chimpanzees eventually moved away, leaving the carcass on the ground (Goodall, 1977). When researchers recovered the body, "both legs and one hand were missing, the abdominal and thoracic cavities were open, and all the intestines gone. The forehead had been bitten into, and part of the brain was missing" (Goodall, 1977, p. 264). This was classified as "partial consumption" because the contents of the thorax and cranium were not completely consumed.

3.1.2 Case 2: 1975 female
As with Case 1, here we summarize the description from Goodall (1977). Observers estimated this female infant to be 1.5–2 years old (Goodall, 1977), but comparison of skeletal and dental maturation to a chimpanzee infant of known age (Andromeda) resulted in an age estimate of 8 months (Kirchhoff, 2010).

In November 1975, a field assistant followed a party of Kasekela chimpanzees (n = 5 adult males, two adult females and their four immature offspring) toward the south of their range. The Kasekela chimpanzees encountered an unknown number of strangers. Most of the Kasekela males chased after and attacked the strangers, while a stranger mother with a female infant and a juvenile of unknown sex climbed a large tree, where she remained trapped until the Kasekela males returned and attacked the stranger female. While being attacked, the female dropped her infant, which was seized by one of the males. After 8 min of seeming to battle for possession of the infant, the mother escaped, bleeding heavily. The infant was flailed against branches and rocks, and displayed with. After this, another male picked up the still-living infant and groomed her. The infant was carried by three different Kasekela chimpanzees for several hours, and then abandoned. A research assistant collected the infant, who died later that evening (Goodall, 1977). The infant was not consumed, though there was opportunity to do so.

3.1.3 Case 3: Rejea
Wilson et al. (2004) described the details of Rejea's death; here we provide a brief overview. On March 30, 1993, observers followed a large party of chimpanzees from the Kasekela community (n = 10 adult males, four adult females, and three younger animals) as they traveled far to the north, into the central range of the Mitumba community. They met a female with a young infant, later identified as Rafiki and her 3-month-old daughter Rejea, based on consultation with observers studying the Mitumba community. Adult males from Kasekela surrounded Rafiki and her infant and attacked, biting Rafiki on her head, ears, fingers, and toes. Rafiki attempted to protect Rejea by holding her close.

Prof (adult male) killed the infant with a bite to the stomach while Rafiki was still holding Rejea. Ten minutes later Prof snatched Rejea from Rafiki. While in possession of the carcass, adult males spent at least 25 min feeding on the body, while others watched. The carcass was also used in a display. Rafiki fled after about an hour, at which point Rejea's carcass was abandoned. The observers collected the carcass, reporting that parts of the abdomen and right arm had been eaten. No further details on order of consumption were described. Necropsy data were not available for Rejea.

3.1.4 Case 4: Andromeda
Andromeda's death has been briefly reported in other studies (Williams et al., 2008; Wrangham, Wilson, & Muller, 2006). Here, we provide details on the events.

On August 13, 2005, observers followed a party of Kasekela chimpanzees (n = 7 adult males, three adolescent males, two mothers with a total of four offspring, four adult females without infants, and an adolescent female) as they traveled into the Mitumba community's range. Meanwhile, another team of observers searched for Mitumba chimpanzees, which had been seen in the area the previous day. At 10:20 hr, Kasekela observers heard calls from Mitumba chimpanzees, and Kasekela chimpanzees began walking in a stalking manner, apparently patrolling for Mitumba chimpanzees. At 10:46 hr, the Kasekela chimpanzees found the Mitumba chimpanzees and began chasing them across the Mitumba stream. By 10:57 hr the Kasekela chimpanzees were attacking the Mitumba chimpanzees, but because the chimpanzees had moved quickly down a steep slope through a region of

dense vegetation, the Kasekela observers did not see details of the attack. At 11:07 hr, Kasekela researchers saw a Mitumba female running quickly; they suspected she had been attacked by Kasekela females. At 11:10 hr, the Kasekela males retreated, chased by two males from the Mitumba community. By this time, observers from the Mitumba site heard the sounds of the attack and ran quickly toward the site, where they encountered three adult females, their offspring, and an adolescent female fleeing from the attack site. The observers continued to run toward the attack site, where they found several members of the Mitumba community near the Mitumba stream, including two adult males, Rudi and Edgar, four adult females, and an adolescent female. A great deal of noise and chaos ensued. Rudi and Edgar displayed, turning over rocks and banging on the buttresses of trees. After some time, observers saw Edgar pick up the body of a dead chimpanzee infant. Edgar displayed with the body, dragging it on the ground. By 11:36 hr, observers had identified the body as that of Andromeda, an infant female from the Mitumba community. At 11:50 hr, Edgar climbed into a tree and rested with it, grooming it. Edgar continued to carry the body until 13:05, when he left it on a tree branch. Adolescent female Bima took the body, which she carried, at one point holding it by the foot as she dragged it on the ground. At times she looked intently at the body and groomed it. Bima continued to carry the carcass until 15:03 hr. At this point the observers collected the body.

From this sequence of events, observers inferred that chimpanzees from the Kasekela community had killed Andromeda, after which males from the Mitumba community retrieved her body.

Chimpanzees did not consume Andromeda, but one of us (JR) described several perimortem wounds during necropsy. These include: a large, deep wound on the medial aspect of the left lower extremity affecting the soft tissues and extending all the way from the inferior, medial side of the thigh to the inguinal area, a wound on the superior aspect of the left foot, a wound on the right hand, two wounds on the lumbar area, wounds near the right eye and right ear, and on the abdominal area. In addition, the right humerus and the frontal bone were fractured (GSRC, unpublished data).

3.2 Taphonomic study

Skeletal analysis allowed us to compare the types of skeletal damage, overall bone survivorship (observed/expected MNE), and which specific elements are represented (% MNE, % NISP) between the chimpanzee infanticide victims documented here and the sample of red colobus prey from Kibale (Pobiner et al., 2007). We also compared chimpanzee infanticide victims with a sample of red colobus prey from Gombe (Plummer & Stanford, 2000) when possible.

3.2.1 Types of skeletal damage

Crenulated edges on the breaks of long bones were common (Figure 1), affecting the majority of recovered long bones. Few skeletal elements exhibited tooth marks or other perimortem surface modifications, though some punctures were evident on the crania of Andromeda (Figure 2) and 1975 Male. Compression fractures to the cranial vault (Figure 3) occurred in all cases except 1975 Female. Incipient fractures on ribs (Figure 4) were evident in all four cases, likely a result of blunt force trauma to the thorax (Pobiner et al., 2007, Fig. 8).

Figure 1 Rejea's humerus with crenulated breaks

Figure 2 Andromeda's frontal bone with punctures

Figure 3 Andromeda's parietal bone with compression fracture

Figure 4 Rejea's rib with incipient fracture

Attackers consumed Rejea for 25 min while Andromeda was not consumed by either her presumed attackers or her natal community. This presented an interesting opportunity to contrast damage accrued to the skeleton during the act of consumption versus only the act of killing. Compression fractures to both crania were evident, which is consistent with the preferred kill method of infanticidal chimpanzees (a bite to the head or abdomen). Because observations indicated that Rejea was killed by an abdominal bite, skull fractures in this case may imply attempts to access the brain, or could have occurred in the context of display behavior that incorporated Rejea's body near her time of death. Incipient rib fractures were also present in both infants, and were possibly the result of display rather than consumption behavior in Andromeda. Both animals also exhibited crenulated breaks on the long bones, though the condition of Andromeda's skeleton obscured break type in some instances. Partial consumption of Rejea's right arm was evident in that researchers did not recover her right humeral midshaft and right radius. The necropsy report described several perimortem wounds for Andromeda. The fracture to the right humerus was evident on the skeleton, but the injury to the left thigh was not (consistent with necropsy observations). Because she was not consumed, Andromeda showed both better bone survivorship and less bone fragmentation than Rejea (Table 2).

Table 2. NISP and MNE for Rejea (RJ), Andromeda (AND), and both infants combined (C), contrasted with red colobus prey data from Pobiner et al. (2007)

Skeletal element	NISP Pobiner	NISP RJ	% total NISP Pobiner	% total NISP RJ	NISP AND	% total NISP AND	NISP C	% total NISP C	MNE Pobiner	%MNE Pobiner	MNE RJ	% MNE RJ	MNE AND	% MNE AND	MNE C	% MNE C
Cranium	126	25	0.31	0.152	24	0.141	49	0.147	33	0.11	1	0.01	1	0.01	2	0.01
Mandible	13	1	0.03	0.006	1	0.006	2	0.006	9	0.03	1	0.01	1	0.01	2	0.01
Clavicle	2	1	0.002469136	0.006	2	0.012	3	0.009	2	0.01	1	0.01	2	0.02	3	0.02
Scapula	9	1	0.02	0.006	2	0.012	3	0.009	6	0.02	1	0.01	2	0.02	3	0.02
Humerus	19	1	0.05	0.006	2	0.012	3	0.009	17	0.06	1	0.01	2	0.02	3	0.02
Radius	14	2	0.04	0.012	2	0.012	4	0.012	14	0.05	2	0.02	2	0.02	4	0.02

Skeletal element	NISP Pobiner	NISP RJ	% total NISP Pobiner	% total NISP RJ	NISP AND	% total NISP AND	NISP C	% total NISP C	MNE Pobiner	%MNE Pobiner	MNE RJ	% MNE RJ	MNE AND	% MNE AND	MNE C	% MNE C
Ulna	13	2	0.03	0.012	2	0.012	4	0.012	13	0.04	2	0.02	2	0.02	4	0.02
Pelvis	16	6	0.04	0.037	6	0.035	12	0.034	13	0.04	2	0.02	2	0.02	4	0.02
Femur	27	3	0.07	0.018	2	0.012	5	0.015	27	0.09	2	0.02	2	0.02	4	0.02
Tibia	25	2	0.06	0.12	3	0.018	5	0.015	25	0.08	2	0.02	2	0.02	4	0.02
Fibula	13	1	0.03	0.006	2	0.012	3	0.009	13	0.04	1	0.01	2	0.02	3	0.02
Carpals/ tarsals	13	2	0.03	0.012	0	0	2	0.006	13	0.04	2	0.02	0	0	2	0.01
Metapodials	10	13	0.02	0.079	15	0.088	28	0.084	10	0.03	10	0.11	15	0.16	25	0.13
Phalanges	18	23	0.04	0.14	33	0.194	56	0.168	18	0.06	23	0.24	22	0.23	45	0.24
Ribs	59	45	0.15	0.274	51	0.3	96	0.287	59	0.2	20	0.21	15	0.16	35	0.18
Vertebrae (cervical, thoracic, lumbar, sacral)	0	36	0	0.22	23	0.135	59	0.177	0	0	24	0.25	23	0.24	47	0.25
Caudal vertebrae	28	n/a	0.07						28	0.09						
Total	405	164			170		334		300		95		95		190	
Cranium	58	1	2	0.57	3.82	1	25	1	24	1	25.5					
Mandible	58	1	2	0.16	1.44	1	1	1	1	1	1					
Clavicle	116	2	4	0.02	1	0.5	1	1	1	0.75	1					
Scapula	116	2	4	0.05	1.5	0.5	1	1	1	0.75	1					
Humerus	116	2	4	0.15	1.12	0.5	1	1	1	0.75	1					
Radius	116	2	4	0.12	1	1	1	1	1	1	1					
Ula	116	2	4	0.11	1	1	1	1	1	1	1					

Skeletal element	NISP Pobiner	NISP RJ	% total NISP Pobiner	% total NISP RJ	NISP AND	% total NISP AND	NISP C	% total NISP C	MNE Pobiner	%MNE Pobiner	MNE RJ	% MNE RJ	MNE AND	% MNE AND	MNE C	% MNE C
Pelvis	58	1	2	0.22	1.23	2	3	2	3	2	3					
Femur	116	2	3	0.23	1	1	1.5	1	1	1.33	1.25					
Tibia	116	2	4	0.22	1	1	1	1	1.5	1	1.25					
Fibula	116	2	4	0.11	1	0.5	1	1	1	0.75	1					
Carpals/ tarsals	870	20	40	0.03	1	0.1	1	0	n/a	0.1	0.05					
Metapodials	290	20	40	0.03	1	0.5	1.3	0.75	1	0.6	1.12					
Phalanges	870	56	112	0.02	1	0.4	1	0.39	1.5	0.4	1.24					
Ribs	1392	26	52	0.04	1	0.77	2.25	0.58	3.4	0.67	2.74					
Vertebrae (cervical, thoracic, lumbar, sacral)	1508	29	58	0	0	0.83	1.5	0.79	1	0.81	1.26					
Caudal vertebrae	1508	n/a	n/a	0.02	1											
Total		170	339	0.04												

1975 Male was partially consumed, and showed patterns of damage qualitatively similar to Rejea's, including incomplete limb bones with crenulated break edges and incipient fractures on ribs. The frontal bone and left parietal had puncture wounds, similar to Andromeda's. 1975 Female was not at all consumed, and showed very little skeletal damage—even compared to Andromeda, the other unconsumed infant. Incipient fractures to some ribs were evident, which, similar to Andromeda, may have been due to display behavior observed near the time of death, but otherwise the skeleton was in good condition and relatively complete for a chimpanzee of this age (approximately 8 months).

The types of skeletal damage evident on all four infanticide cases described here were similar to skeletal damage recorded for red colobus prey from Kibale (Pobiner et al., 2007), including crenulated edges of long bones, incipient fractures on ribs, compression fractures and tooth punctures of the cranial vault, and few/no tooth scores and notches (Pobiner et al., 2007) The scapulae and ossa coxae showed crenulated or frayed edges of breaks in both monkey prey and the chimpanzee infants. In the cases presented here, however, the damage to the ossa coxae and scapulae was less extensive in the chimpanzee infants. While glenoid fossae in the prey sample were typically missing and possibly consumed, damage in the chimpanzee infants was restricted to the

blade in the three recovered scapulae from Andromeda and Rejea. All parts of the os coxa were recovered for both chimpanzee infants, but only the ilium was recovered from the red colobus prey sample.

3.2.2 Bone fragmentation

Bone fragmentation (NISP/MNE) in Andromeda and Reja was often similar to the red colobus sample from Kibale (Table 2). Bone fragmentation in Rejea was generally higher than in the un-consumed Andromeda. Bone fragmentation levels were influenced by skeletal immaturity of the two chimpanzee infants, both of which had unfused crania and pelves. Calculated fragmentation for these two elements was higher than the red colobus sample, but because approximately one-third of the red colobus sample consisted in adults, direct comparison of these figures was not possible. We therefore considered bone survivorship a better skeletal measure of degree of consumption.

3.2.3 Bone survivorship

The assemblage of bones from the two infanticide victims with quantitative data (Andromeda and Rejea) was dominated (% Number of Identified Specimens) by axial skeletal elements (skull, ribs, vertebrae), and small bones of the distal extremities (e.g., phalanges). Appendicular elements, particularly the long bones, were also commonly recovered. Table 2 gives MNE and NISP values for Rejea, Andromeda, and both infants combined. Both 1975 Male and 1975 Female included cranial and other axial skeletal elements as well as appendicular skeletal elements.

One of the most drastic differences between the prey sample and the chimpanzee infant sample was that Pobiner et al. (2007) reported no pre-caudal vertebrae from the hunted red colobus sample (n = 58 individuals, MNE = 300), while vertebrae (bodies and laminae) made up a significant portion of the chimpanzee infant sample, with a MNE of 47, or 25% of the identified specimens (see Table 3). In addition, phalanges made up a higher %MNE in chimpanzee infants (24%) than in the prey sample [6% (Pobiner et al., 2007)], and chimpanzee infant long bone ends were less commonly consumed compared to the prey sample. Overall, there was better bone survivorship (observed/expected MNE) of nearly all skeletal elements in both chimpanzee infants (Table 3) than in the prey sample (Pobiner et al., 2007).

Table 3. Summary of degree of consumption of chimpanzee infanticide victims. Cases are sorted by date of observation.

Infant sex	Infant age	Date of Attack	Site	Type	Sex of attacker(s)	Consumption	Reference
Female	3 months	14-Feb-65	Gombe	Unknown	?	Not consumed, no opportunity for consumption	Williams et al. (2008)
Unknown	Newborn	13-Nov-67	Budongo	Intercommunity	M	Partial consumption, but degree uncertain	
Unknown	1.5 years ?	1-Sep-71	Gombe	Intercommunity	M	Partial consumption, voluntary abandonment	Bygott (1972)
Male?	3 years?	25-Apr-74	Mahale	Intercommunity	M	Complete consumption, including at least some skeletal elements	Nishida et al. (1979)

Infant sex	Infant age	Date of Attack	Site	Type	Sex of attacker(s)	Consumption	Reference
Female	3 weeks	15-Aug-75	Gombe	Intracommunity	F	Partial consumption, voluntary abandonment (thorax and abdomen uneaten)	Goodall (1977)
Male	1.5-2 yearsa (9 months)	30-Sep-75	Gombe	Intercommunity	M	Partial consumption, voluntary abandonment	Goodall (1977) (1975 Male)
Female	1.5-2 yearsa (8 months)	2-Nov-75	Gombe	Intracommunity	M	Not consumed, voluntary abandonment	Goodall (1977) (1975 Female)
Unknown	3 weeks	8-Jan-76	Gombe	Intracommunity	F	Not consumed, no opportunity for consumption (recovered by mother)	Goodall (1977)
Male	3 weeks	22-Oct-76	Gombe	Intracommunity	F	Complete consumption, including at least some skeletal elements	Goodall (1977)
Female	3 weeks	21-Nov-76	Gombe	Intracommunity	F	Partial consumption, but degree uncertain	Goodall (1986)
Male	2.5 months	13-Jan-77	Mahale	Intracommunity	M	Complete consumption, including at least some skeletal elements	Norikoshi (1982)
Unknown	1.5-2.5 years	20-Mar-79	Gombe	Intercommunity	M	Partial consumption, but degree uncertain	Goodall (1986)
Unknown	Newborn	14-Jun-79	Mahale	Intracommunity	mixed	Complete consumption, including at least some skeletal elements	Kawanaka (1981)
Male	Neonate	5-Jul-83	Mahale	Intracommunity	M	Complete consumption, including at least some skeletal elements	Takahata (1985)
Male	3 months	15-Dec-83	Mahale	Intracommunity	mixed	Complete consumption, including at least some skeletal elements	Nishida and Kawanaka (1985)

| Infant sex	Infant age	Date of Attack	Site	Type	Sex of attacker(s)	Consumption	Reference
Male	0.83	16-Jul-85	Mahale	Intracommunity	M	Not consumed, no opportunity for consumption (mother retained)	Hamai et al. (1992)
Male	5–6 months	3-Oct-89	Mahale	Intercommunity	M	Complete consumption, including at least some skeletal elements	Hamai et al. (1992)
Male	5–6 months	24-Jul-90	Mahale	Intracommunity	M	Partial consumption, but degree uncertain	Hamai et al. (1992)
Male	1.49 years	10-Jan-91	Gombe	Intracommunity	M	Not consumed, no opportunity for consumption	Williams et al. (2008), Wrangham et al. (2006)
Female	3 months	30-Mar-93	Gombe	Intracommunity	M	Partial consumption, voluntary abandonment	Wilson et al. (2004) (Rejea)
Male	Neonate	29-Oct-93	Mahale	Intracommunity	?	Not consumed, voluntary abandonment	Hosaka et al. (2000)
Unknown	2 months	17-Feb-94	Gombe	Intracommunity	F	Partial consumption, but degree uncertain	Pusey et al. (2008)
Unknown	Unknown	2-Feb-95	Budongo	Intercommunity	m	Complete consumption, including at least some skeletal elements	Newton-Fisher (1999)
Male	Unknown	29-Sep-95	Budongo	Intercommunity	M	Partial consumption, voluntary abandonment	Newton-Fisher (1999)
Male	2 years	14-Dec-96	Kibale	Intracommunity	1M, 1F	Not consumed, no opportunity for consumption (mother retained)	Arcadi and Wrangham (1999)
Female	1 year	29-Oct-98	Gombe	Intercommunity	M	Partial consumption, but degree uncertain	Wilson et al. (2004)
Unknown	Unknown	3-Apr-99	Kibale	Intercommunity	M	Complete consumption, including at least some skeletal elements	Watts and Mitani (2000)

Infant sex	Infant age	Date of Attack	Site	Type	Sex of attacker(s)	Consumption	Reference
Unknown	Unknown	28-Jun-99	Kibale	Intercommunity	M	Complete consumption, including at least some skeletal elements	Watts and Mitani (2000)
Unknown	2?	5-Jul-00	Kibale	Intracommunity	M	Uncertain	Watts et al. (2002)
Male	2.5 years	12-Dec-00	Mahale	Intercommunity	M	Uncertain	Kutsukake and Matsusaka (2002)
Male	unknown	8-Sep-02	Taï	Intercommunity	M	Not consumed, voluntary abandonment	Boesch et al. (2008)
Unknown	1 week	12-Mar-04	Budongo	Intercommunity	F	Not consumed, voluntary abandonment	Townsend et al. (2007)
Male	Ventral clinger	6-Oct-04	Kibale	Intercommunity	M	Partial consumption, but degree uncertain.	Sherrow and Amsler (2007)
Male	Not indicated / known	12-Oct-04	Kibale	Intercommunity	M	Partial consumption, but degree uncertain.	Sherrow and Amsler (2007)
Unknown	Ventral clinger	12-Oct-04	Kibale	Intercommunity	M	Not consumed, voluntary abandonment	Sherrow and Amsler (2007)
Female	9 months	13-Aug-05	Gombe	Intracommunity	mixed?	Not consumed, no opportunity for consumption (rescued by natal group)	This study, GSRC unpublished data (Andromeda)
Unknown	1 week	3-Feb-06	Budongo	Intercommunity	F	Not consumed, voluntary abandonment	Townsend et al. (2007)
Unknown	Neonate	2-Jul-06	Budongo	Intracommunity	F	Partial consumption, but degree uncertain	Townsend et al. (2007)
Male	2.2 years	18-Nov-06	Gombe	Intracommunity	F	Not consumed, voluntary abandonment	Williams et al. (2008)
Unknown	Unknown	Not reported	Taï	Intracommunity?	F?	Partial consumption, but degree uncertain	Boesch and Boesch-Achermann (2000)

- a Indicates that the age reported in the original publication is an estimate that has more recently been reassessed (reassessed age appears in parentheses).

Similarly, Plummer and Stanford (2000) reported that "ribs and vertebrae rarely survive chimpanzee consumption" (p. 353), and the skeletal sample they analyzed (*n* = 5 red colobus) exhibited many of the same trends as the assemblage from Kibale. There were no hand or foot bones in the red colobus prey sample from Gombe, and vertebral survivorship was much lower than in the chimpanzee infants (observed/expected MNE for all vertebrae = 20%, but all vertebral elements were from a single monkey) (Plummer & Stanford, 2000).

Better survivorship of vertebrae, metapodials, and phalanges in the chimpanzee infanticide victims compared to red colobus prey (Figure 5) indicated a decreased degree of consumption of these two infanticide victims compared to red colobus prey documented by both Pobiner and colleagues (2007) and Plummer and Stanford (2000). This pattern was consistent in both the partially consumed infant (Rejea) as well as the unconsumed infant (Andromeda).
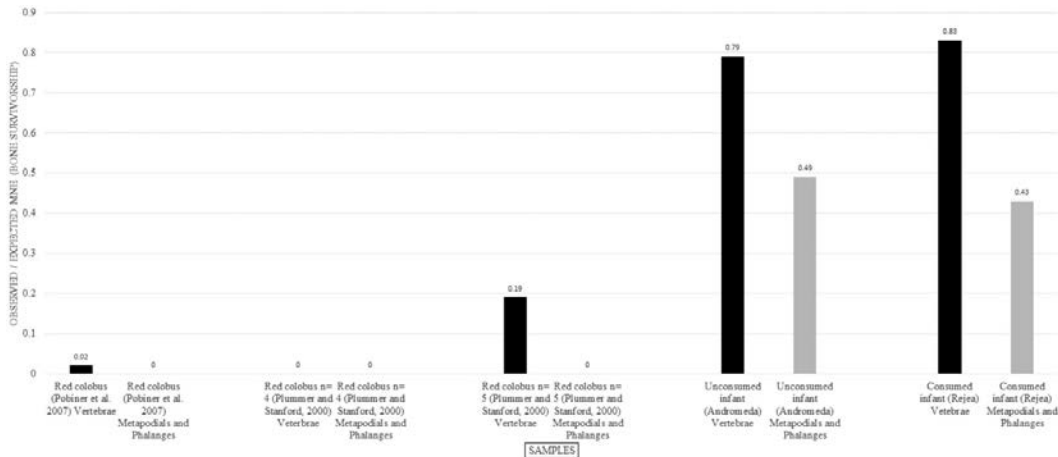
Figure 5 Bone survivorship of vertebrae and phalanges in monkey prey versus chimpanzee infanticide victims

3.2.4 Published descriptions of infanticides

Our review of infanticide cases (*n* = 40) revealed that infant chimpanzees are consumed completely in only 23% of cases, and not consumed at all in 33% of cases (Table 3, Figure 6). This may be because the infant is simply abandoned without being consumed (*n* = 7: Boesch et al., 2008; Goodall, 1977; Hosaka, Matsumoto-Oda, Huffman, & Kawanaka, 2000; Sherrow & Amsler, 2007; Townsend, Slocombe, Thompson, & Zuberbuhler, 2007 (*n* = 2); Williams et al., 2008) or because the mother or other members of the natal group recovered the infant (n = 6: Arcadi & Wrangham, 1999; Goodall, 1977; GSRC, unpublished data (Andromeda); Hamai et al., 1992; Williams et al., 2008; Wrangham et al., 2006). Of the 15 cases of partial consumption, 10 (25% of the total cases) do not indicate the degree to which the infant was consumed. In the other five cases (10% of the total cases), the carcass was voluntarily abandoned. In no cases was the carcass involuntarily abandoned once feeding commenced.

- ▪ Partial consumption, voluntary abandonment (12%)
- ▪ Partial consumption, forced abandonment (0%)
- ▪ Complete consumption, including at least some skeletal elements (25%)
- ▪ Partial consumption, but degree uncertain (25%)
- ▪ Not consumed, voluntary abandonment (18%)
- ▪ Not consumed, no opportunity for consumption (15%)
- ▪ Uncertain (5%)
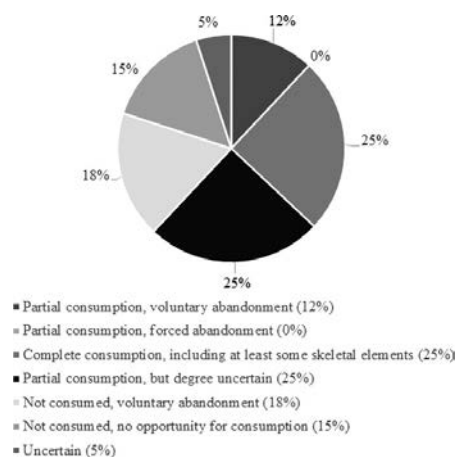
Figure 6 Degree of consumption documented in cases (*n* = 40) of chimpanzee infanticide

4 DISCUSSION

The results presented here are necessarily of a preliminary nature due to the small sample size, but we hope this study encourages others to preserve and study similar skeletal materials whenever possible at long-term primate behavioral research sites. We examined skeletal damage to chimpanzee infanticide victims and reviewed published cases of infanticide to shed additional light on whether the exploitation hypothesis is sufficient to explain infanticidal behavior in chimpanzees. If so, we would expect that types of damage, bone fragmentation, and bone survivorship documented by the taphonomic study would be similar to that of red colobus prey documented by Pobiner and colleagues (2007). If the exploitation hypothesis holds true, we would also expect that the review of chimpanzee infanticide cases would demonstrate that infanticide victims are completely consumed (as defined by Plummer & Stanford, 2000; Stanford, 1998; Teleki, 1973) just as often as red colobus prey.

Types of skeletal damage to red colobus prey and chimpanzee infanticide victims were similar. Both were characterized by crenulated fractures on long bones, damage to ribs (e.g., from flailing), punctures to the cranial vault, and good survivorship of crania (Plummer & Stanford, 2000; Pobiner et al., 2007).

Bone fragmentation (NISP/MNE) measures between the two samples (chimpanzee infants and red colobus prey) were not entirely comparable due to possible differences in skeletal maturation (the red colobus prey sample was composed of mostly sub-adults, but approximately one-third of the individuals represented in the sample were adults). Identified cranial specimens, for example, might have derived from unfused sub-adult crania or fractured pieces of the cranium from any age animal. Sample size also strongly influenced %NISP, as there were only two infant chimpanzees with quantitative data available (e.g., this chimpanzee infant sample could never include more than four femora, and the red colobus sample included more than four of each type of long bone).

Bone survivorship provided more information, as it was based on the observed versus expected number of skeletal elements for each animal/group of animals. Survivorship was higher both for partially consumed Rejea as well as unconsumed Andromeda compared to the red colobus sample. This was particularly striking for the cranium, which is often consumed/destroyed while accessing and ingesting the brain, and for hand and foot bones. Behavioral observations have indicated that hands and feet are often consumed first in cases of both infanticide and hunting (Hamai et al., 1992; Kawanaka, 1982; Nishida et al., 1979; Takahata et al., 1984; Teleki, 1973), and hand/foot bones from monkey prey have been recovered from chimpanzee fecal material (Tappen & Wrangham, 2000). Carpals/tarsals, metapodials, and phalanges had better survivorship in these two chimpanzee infants than the red colobus sample. The red colobus sample also included no pre-caudal vertebrae (Pobiner et al., 2007), where the partially consumed Rejea had a vertebral survivorship rate of 0.83.

Rejea showed better bone survivorship than Andromeda for some skeletal elements (e.g., vertebrae), despite Andromeda being older and unconsumed. Preservation bias likely affected Andromeda's skeleton more than Rejea's. Andromeda's cortical bone is very friable, suggesting that some skeletal elements may have been completely lost to decomposition during burial for soft tissue removal. This is probably due to the amount of time the body remained buried (3 years, 10 months). Rejea's skeleton was exhumed prior to 2008, but specific data on exhumation timing are not available; it is likely that Rejea's skeleton spent less time in the ground than Andromeda's.

We examined bone survivorship rates for both Rejea and Andromeda as a reflection of the fact that chimpanzee infanticide victims are not always consumed (Table 3). It should be noted, however, that some observations of infanticide described the complete consumption of the infant (including skin, hair, and bones) and that the chimpanzee infant included in the Pobiner et al. (2007) study was represented by only four cranial fragments (B. Pobiner, personal communication, 2009). Examining the 40 reported cases of directly observed chimpanzee infanticides published to date may therefore provide additional insight into whether the exploitation hypothesis applies to chimpanzee infanticide.

Monkey prey are seldom abandoned without being consumed; observed cases of abandonment include the capture of non-preferred prey (infants or sub-adults are preferred as prey by most chimpanzee populations [Nishida et al., 1979; Pobiner et al., 2007; Stanford, 1998; Stanford et al., 1994a)]) and when multiple monkeys are captured in a single hunt (Plummer & Stanford, 2000). Otherwise, "chimpanzees typically entirely consume their prey, including the bones" (Plummer & Stanford, 2000, p. 348). This does not seem to be the case for chimpanzee infanticides, where complete consumption occurred in only 23% of cases. Even if we assumed complete consumption for the cases in which we know the infant was at least partially consumed, but the degree of consumption was not indicated/observed (n = 10), still just half of all observed infanticides would include complete consumption of the infant's carcass. This seems to stand in contrast with typical consumption behavior of red colobus prey at Gombe (Goodall, 1986; Plummer & Stanford, 2000; Stanford, 1998; Teleki, 1973). Also, while consumption of chimpanzee infants can involve ingestion of the entire body, it has been alternately described as being less complete and/or more intermittent than the consumption of monkey prey (Newton-Fisher, 1999; Sherrow & Amsler, 2007).

Demographic differences between infanticide events may also be relevant. While infanticide victims that were completely consumed (n = 10) as well as those that were partially consumed and voluntarily abandoned (n = 6) were split roughly evenly between inter- and intracommunity infanticide cases, all cases where the infant was not consumed and in which there was no opportunity for consumption (n = 6) were cases of intracommunity infanticide. In addition, complete consumption of the infant may be more common when males commit infanticide versus females. Of the 10 cases in which complete consumption of the infant was documented, seven involved infanticidal males, two involved male and female attackers, and the last case involved only female attackers, but a mixed-sex group which fed on the carcass. Additional and more detailed documentation of infanticide in chimpanzees is needed to further examine these possible trends.

While the data presented here do not support the exploitation hypothesis as the most parsimonious explanation for chimpanzee infanticide, chimpanzees undoubtedly accrue nutritional benefits from consuming infanticide victims. This study is limited by sample size as well as contrasting bone survivorship in infanticide victims from Gombe versus red colobus prey from Kibale, but it does suggest that the exploitation hypothesis only incompletely explains chimpanzee infanticide. Killing infants directly eliminates competitors, reduces future coalition size of rival groups (if the victim is male), and likely deters mothers from using the parts of their range where their infants have been attacked, circumstances which provide support for the resource competition hypothesis. Hard tissues may provide an additional line of evidence for determining the adaptive significance of infanticide in chimpanzees, and can aid in our more complete understanding of primate behavior in general. Especially valuable are skeletal data that can be matched with behavioral data, as is the case for the Gombe chimpanzees and other long-term primate research sites. We encourage the recovery and preservation of

skeletal material from these contexts wherever possible, and continued research on how behavior affects the skeleton.

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