

Morphological Identification of Hair Recovered from Feces for Detection of Cannibalism in Eastern Chimpanzees

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Keywords

Microscopy · Forensics · Guard hair · Infanticide · *Pan troglodytes*

Abstract

Chimpanzees (*Pan troglodytes*) are primarily frugivorous but consume a variable amount of meat from a variety of organisms, including other chimpanzees. Cannibalism is rare, usually follows lethal aggression, and does not occur following natural deaths. While chimpanzee cannibalism has been documented at multiple sites, many instances of this behavior go unrecorded. Identification of chimpanzee remains in feces, however, can provide indirect evidence of cannibalism. Hair, in particular, typically passes through the gastrointestinal tract undamaged and is commonly used for purposes of identification in wildlife forensics. Here we test the hypothesis that eastern chimpanzee (*Pan troglodytes schweinfurthii*) guard hair morphology can be reliably distinguished from the hairs of their most common prey species. Methods and results are presented in the context of a case study involving a suspected chimpanzee infanticide from Gombe, Tanzania. We find that chimpanzee guard hair morphology is unique among tested mammals and that the presence of abundant chimpanzee hair in feces is likely the result of cannibalism and not incidental ingestion from grooming or other means. Accordingly, morphological analysis of guard hairs from feces is a promising, cost-effective tool for the determination of cannibalistic acts in chimpanzees.

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Introduction

Chimpanzees (*Pan troglodytes*) are habitual, but infrequent, meat eaters who primarily hunt red colobus monkeys (*Piliocolobus* or *Procolobus* spp.) if available, but can be opportunistic in prey acquisition, hunting mammalian prey as diverse as primates, bushpigs, rodents, and bushbucks [Uehara, 1997; Newton-Fisher, 2014; Gilby et al., 2017]. On occasion, chimpanzees also prey upon conspecifics, though context suggests lethal conspecific aggression is not motivated by meat acquisition. Instead lethal aggression is likely adaptive in that it removes competitors [Goodall, 1986; Wrangham, 1999; Townsend et al., 2007; Pusey et al., 2008; Mitani et al., 2010; Wilson et al., 2014]. Importantly, lethal aggression is not always followed by cannibalism (the consumption of chimpanzee flesh) nor is the victim always fully consumed.

Lethal aggression against conspecifics most commonly occurs during intergroup encounters where adult males, and less frequently females and juveniles, are sometimes killed [Watts et al., 2002, 2006; Boesch et al., 2008; Williams et al., 2008; Mitani et al., 2010; Wilson et al., 2014]. Evidence suggests that lethal intercommunity aggression is a means through which a chimpanzee community can expand its range and improve access to resources by acquiring new territory and decreasing chimpanzee density throughout the range [Goodall, 1986; Mitani et al., 2010; Wilson et al., 2014]. Intragroup lethal aggression, usually against males, also occasionally occurs [Kaburu et al., 2013; Wilson et al., 2014; Pruettz et al., 2017], though is less understood. Finally, both males and females commit intracommunity infanticide [e.g., Goodall, 1977; Takahata, 1985; Hamai et al., 1992; Arcadi and Wrangham, 1999; Watts and Mitani, 2000; Townsend et al., 2007; Pusey et al., 2008; Wilson et al., 2014; Nishie and Nakamura, 2017] though the proposed motivation and victim selection differ markedly between the sexes. Males target infants that they suspect are not their own in a sexually selected strategy that hastens the onset of female receptivity [Hrdy, 1979]. They usually attack infants in their first year of life [Wilson et al., 2015] but have been observed attacking infants as old as 4 years [Murray et al., 2007]. In contrast, infanticide by females is usually restricted to the first 2 months after an infant's birth and is likely driven by long-term resource competition, whereby females eliminate a future competitor and gain access to resources that would otherwise be used by the victim [Goodall, 1977; Townsend et al., 2007; Pusey et al., 2008]. Victims of infanticide are frequently cannibalized to some degree and may be shared with family members or group mates [e.g., Bygott, 1972; Goodall, 1977; Nishida et al., 1979; Takahata, 1985; Hamai et al., 1992; Watts and Mitani, 2000]. In contrast, adult victims are only occasionally (and partially) consumed [Goodall, 1986; Pruettz et al., 2017].

Rare events, such as lethal aggression against conspecifics, are difficult to quantify in chimpanzees because of the fission-fusion social system where all members of the community are infrequently, if ever, all together. Subgroup (or party) composition changes on an hourly to daily basis, and many events and behaviors go undetected when individuals or parties are not under observation. Therefore, methods that allow for the detection of particular events without direct observation will aid in quantifying and understanding uncommon behaviors such as lethal aggression and cannibalism.

In 2007, in Gombe National Park, Tanzania, researchers came upon a party of agitated chimpanzees and observed a low-ranking female without her newborn infant. Later that morning, a high-ranking female deposited a fecal sample that con-

tained a large amount of hair and was unusually dark. Circumstantial evidence (discussed below in the “Researcher’s Account”) suggested that the source of the hair may have been an infant chimpanzee. Researchers collected the sample and placed it in formalin fixative, precluding genetic identification of the hair source. Hair morphology, however, is commonly used in wildlife forensics to identify animals [e.g., Knecht, 2012] and diagnostic features remain intact even after passing through the gastrointestinal tract [Quadros and Monteiro-Filho, 1998]. To our knowledge, 2 previous studies have investigated chimpanzee hair morphology for purposes of identification following recovery from feces [Inagaki and Tsukahara, 1993; Bakuneeta et al., 1993]. Both studies utilized scanning electron microscopy to examine scale pattern and medulla microstructure to positively identify chimpanzee hairs, but neither study presented sufficient information on comparative taxa for readers to differentiate chimpanzee hair morphology from other mammals based on either the examined features or more basic morphological traits.

Here we investigate the source of the hairs in the fecal sample of interest by testing the hypothesis that eastern chimpanzee (*Pan troglodytes schweinfurthii*) guard hair morphology can be reliably distinguished from the hairs of 7 prevalent chimpanzee prey species using morphological features that can be evaluated macroscopically or microscopically with inexpensive materials (i.e., using methods that can be performed in the field). We then discuss the implications of our findings for understanding chimpanzee behavioral ecology and the utility of our methods for identifying cannibalistic acts.

Materials and Methods

Study Site and Behavioral Data Collection

Gombe National Park is located in Western Tanzania (4.6667° S, 29.6333° E), bounded by Lake Tanganyika to the west and a rift escarpment 1,500 m above the lake to the east. Three chimpanzee communities reside within the park. The central Kasekela community has been habituated since the 1960s, and systematic focal data collection, initiated in 1970, continues to the present. In October 2007, the Kasekela community included 22 adult females, 12 adult males, and 24 pre-adults. Each day, pairs of field assistants follow a single individual from dawn to dusk and record party composition and location continuously, as well as a narrative account of the focal individual’s behavior. Aggressive events and dominance interactions for all group members are also recorded. Because of the fission-fusion social system, each individual is not necessarily seen on a daily basis, and some individuals can travel independently of the observed group for extended periods. Permission to conduct chimpanzee behavioral observations and collect fecal samples was granted by Tanzania National Parks, the Tanzanian Wildlife Research Institute, and the Tanzanian Council for Science and Technology.

Event Summary

Researcher’s Account

At 6:50 a.m. on October 18, 2007, field assistants, including G. Paulo, heard a chorus of pant hoot calls and screams coming from a nearby valley and made their way to the location of the noise. At 7:20 a.m., the field assistants found a large party of chimpanzees including 8 adult females, 9 adult males, and 15 pre-adults. The party was scattered and moving east. At 8:09 a.m., a second chorus of pant hoots, screams, and tree-drumming broke out to the east. Among the chimpanzees in this party were low-ranking female Schweini, who had just given birth to her first offspring 4 weeks earlier, and high-ranking female Fanni, with her 2 dependent offspring and adolescent son. At 8:45 a.m., G. Paulo first noticed Schweini without her newborn offspring. She

appeared weak, though no wounds were evident. Schweini was acting fearfully in the presence of Fanni and kept her distance throughout the day. From 8:45 to 9:35 a.m., Fanni groomed her infant daughter, Familia, and the group continued to pant hoot and drum on trees. At 9:30 a.m., Fanni defecated. G. Paulo noted many hairs in the abnormally dark feces and collected a sample.

Hair and Fecal Analysis

From January 2006 to January 2008, fecal samples were collected opportunistically as part of a study to identify patterns of parasitism in the Gombe chimpanzees [Gillespie et al., 2010]. These samples were taken from freshly deposited feces and were immediately placed in 15 ml of 10% formalin fixative in ParaPak[®] containers (Meridian Bioscience, Cleveland, OH, USA). In 2007, samples were collected from a total of 79 individuals and, on average, 6.9 samples of varying mass were collected per individual per year (range: 1–15 samples) over the course of the study [Gillespie et al., 2010].

The sample collected from Fanni's atypical excrement on the morning of October 18, 2007, had a mass of 10.3 g (after accounting for 15 g of formalin solution) when examined for the purposes of this study. Though the total fecal mass is unknown, the mean chimpanzee fecal mass calculated by Lambert (2002) is 109 g. Thus, the collected sample likely represents only a small portion of the total deposit. Twenty-four guard hairs (henceforth referred to as target hairs; solid black [$n = 18$] or solid white [$n = 6$]) were identified in the sample, and each was retrieved, rinsed in distilled water, and air dried. DNA degradation due to formalin fixative prevented genetic analysis; however, the target hairs were in suitable condition for morphological examination [guided by Deedrick and Koch, 2004a, b; Knecht, 2012].

Fanni's party was observed successfully hunting on both October 15 (multiple red colobus monkeys) and 16 (2 bushpigs), though Fanni was not seen eating any of the kills. Nevertheless, for comparative purposes we conservatively included in the present study the hairs of the most common mammalian prey species of chimpanzees at Gombe National Park (and, thus, the most likely sources of the target hairs) plus chimpanzees (both immature and mature). Seven non-chimpanzee species of mammals found at or near Gombe National Park were identified as species of interest: blue monkeys (*Cercopithecus mitis*), red-tailed monkeys (*Cercopithecus ascanius*), vervet monkeys (*Chlorocebus aethiops*), olive baboons (*Papio anubis*), red colobus (*Piliocolobus* or *Procolobus* spp.), bushpigs (*Potamochoerus larvatus*), and bushbucks (*Tragelaphus scriptus*). Red colobus are, by far, the preferred prey of the Gombe chimpanzees, followed by (in order) bushpigs, bushbucks, baboons, and other monkey species [Goodall, 1986; Wrangham and Bergmann Riss, 1990]. Guard hairs were harvested from the dorsal and ventral surfaces of the thorax, limbs, and head of pelts housed at the National Museum of Natural History, Washington, DC, USA, from 5 individuals of each primate taxon, 3 bushbucks, and 1 bushpig.

Hairs were first examined macroscopically and sorted by color and the presence/absence of banding. Five randomly selected guard hairs per individual comparative specimen – with at least 1 representative hair from (1) the limbs, (2) the head, and (3) the dorsal/ventral surfaces – and 10 randomly selected target hairs were mounted on glass slides with Cytoseal 280. Medulla structure, margins, width (μm), and midshaft diameter (μm) were examined on an Olympus BX40 microscope and micrographed with an Olympus DP25 camera using cellSens software [see Moore et al., 1974, and Teerink, 1991, for more information on the hair medulla descriptions used in this study].

The target hairs were further compared to chimpanzee hairs with a focus on cuticle scale patterns and cross-sectional shape. Ten additional randomly selected target hairs and 2 randomly selected thoracic hairs each from 4 individual chimpanzees (2 mature and 2 immature) were secured by carbon tape on aluminum stubs and imaged on an FEI XL-30 environmental scanning electron microscope at 20 kV. Micrographs of each hair were acquired at a magnification of $\times 5,000$, and cuticle scale type was assessed. Cuticle scale patterns change proximodistally along the guard hair shaft [Seiler, 2010]. Accordingly, environmental scanning electron microscope analyses favored complete target hairs where the midshaft could be determined, facilitating comparisons across individual guard hairs. The same hairs were then placed in a thin layer of clear nail polish on a glass slide. The polish was allowed to dry for 10 min, and the hairs were removed from the slide, leaving an impression of the cuticle scale in the dried polish. The scale casts were

Table 1. Macro- and microscopic morphological features of guard hairs by taxon

Taxon	Colors	Banded	Medulla structure(s) ¹	Medulla margins ¹	Medulla width ²
<i>Cercopithecus ascanius</i>	gray, red-brown, white	yes	ladder; unbroken cellular	scalloped; fringed	variable
<i>Cercopithecus mitis</i>	blue-gray, black, white, brown	yes	ladder; unbroken cellular	scalloped; fringed	variable
<i>Chlorocebus aethiops</i>	gray, white, light and dark brown	yes	ladder; unbroken cellular	scalloped; fringed	variable
<i>Pan troglodytes</i>	black, dark and light brown, white	no	mostly continuous	amorphous	narrow
<i>Papio anubis</i>	yellow-brown, dark brown, black	yes	ladder; unbroken cellular	scalloped; fringed	variable
<i>Ptilocolobus/ Procolobus</i> spp.	dark gray, red-brown, red, white	no	ladder; unbroken cellular	scalloped; fringed	narrow
<i>Potamochoerus larvatus</i>	red-brown, black, white	no	mostly continuous	globular; amorphous	variable
<i>Tragelaphus scriptus</i>	red-brown, black, white	no	continuous	straight	wide
Target	black, white	no	mostly continuous	amorphous	narrow

¹ Medullae in all species were variable. Only the most commonly observed medulla structures and margins are listed. ² Wide, >50% of total hair width; narrow, <50% of total hair width.

examined and micrographed on the aforementioned Olympus microscope and camera. Three target and chimpanzee hairs were later frozen at -22°C in Tissue-Tek OCT, sectioned into 10- μm slices on a Leica CM3050S cryostat, mounted, and examined with a light microscope to evaluate cross-sectional shape.

All fecal samples collected within the 5-day period following October 18, 2007, and belonging to Kasekela chimpanzees present in the large party with Fanni on the morning of note ($n = 8$), were macroscopically examined for traces of hair. These samples were deposited by 1 adolescent male, 1 juvenile male, 3 adult females with infants at the time (including Schweini), 2 juvenile females, and 1 infant female. Six fecal samples belonging to Fanni collected ± 14 weeks from October 18, 2007 were also inspected for hair to establish a baseline for the presence of hair in her excrement.

Results

The target hairs are differentiated from all comparative taxa hairs, except chimpanzees, by one or more of the evaluated characteristics visible macroscopically or with a light microscope (Fig. 1; Table 1). While all target hairs are unbanded, all comparative primate guard hairs exhibit some banding, with the exception of chimpanzees and red colobus monkeys. The medullae of the target hairs are generally continuous and narrow with smooth, amorphous margins; however, some specimens possess an interrupted (mostly continuous, but with some breaks) medulla,

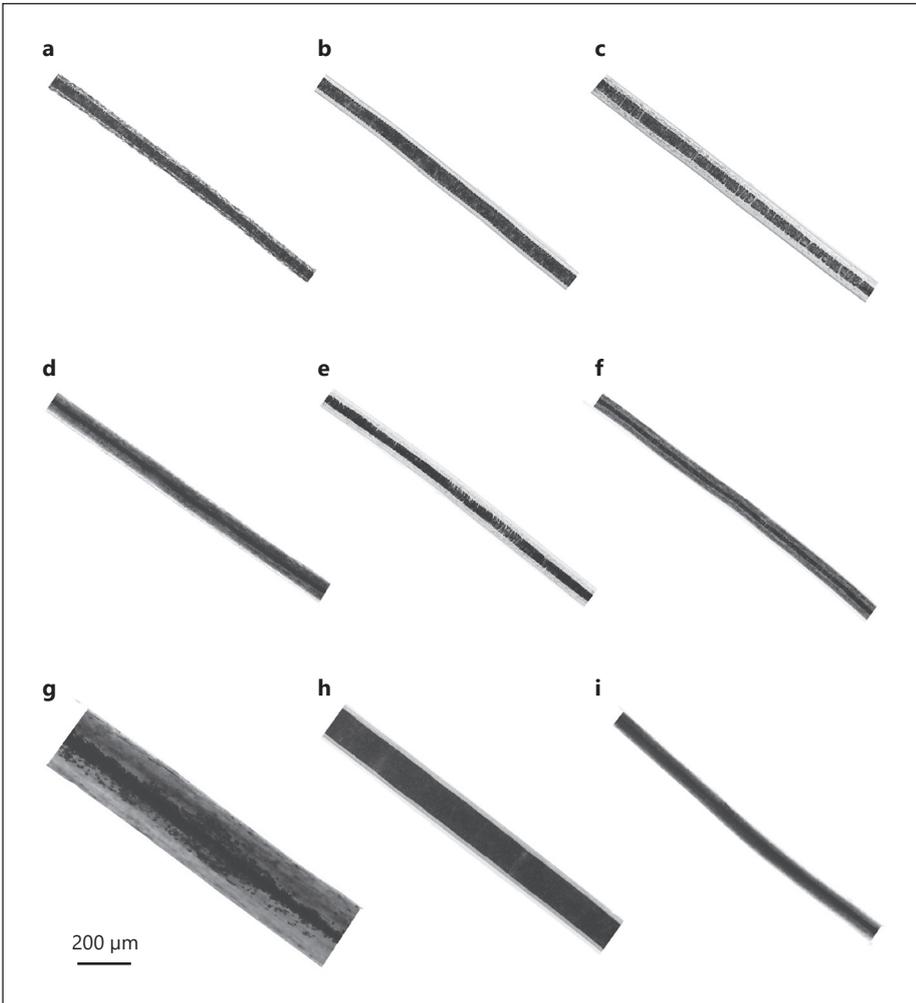


Fig. 1. Example guard hairs of select mammal taxa found in Gombe National Park, Tanzania (**a-h**), plus target hair (**i**) under a light microscope. **a** Red-tailed monkey (*Cercopithecus ascanius*) – wide unbroken cellular medulla with scalloped margins. **b** Blue monkey (*Cercopithecus mitis*) – wide unbroken cellular medulla with scalloped margins. **c** Vervet (*Chlorocebus aethiops*) – mid-width uniserial ladder and unbroken cellular medulla with scalloped and fringed margins. **d** Chimpanzee (*Pan troglodytes*) – narrow continuous medulla with amorphous margins. **e** Olive baboon (*Papio anubis*) – mid-width mostly unbroken cellular medulla with fringed margins. **f** Red colobus monkey (*Piliocolobus/Procolobus* spp.) – narrow mostly unbroken cellular medulla with variably scalloped margins. **g** Bushpig (*Potamochoerus larvatus*) – narrow continuous medulla with globular and amorphous margins. **h** Bushbuck (*Tragelaphus scriptus*) – wide continuous medulla with straight margins. **i** Target hair – narrow continuous medulla with amorphous margins.

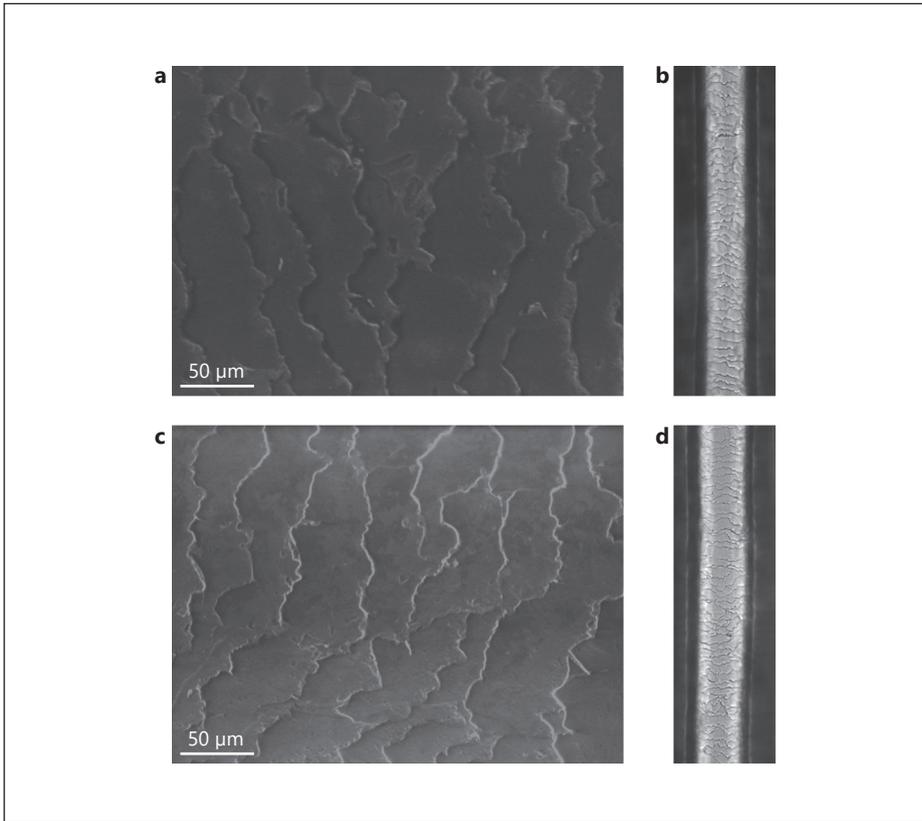


Fig. 2. Cuticle scale micrographs. Environmental scanning electron micrographs of target hair (a) and immature chimpanzee hair (c) taken at a magnification of $\times 5,000$. Light micrographs of target (b) and immature chimpanzee (d) hair cuticle casts at a magnification of $\times 100$. Hairs imaged near midshaft. Both target and chimpanzee hairs have imbricate cuticle scales with a wave pattern and (mostly) rippled margins.

while others are missing a medulla entirely. This is consistent with the hair of chimpanzees, which exhibit a similar pattern of variation. Notably, more immature chimpanzee hairs lack a visible medulla than do adult chimpanzee hairs. In contrast, the medullae of comparative monkey specimens (red colobus, blue, red-tailed, and olive baboons) are also variable, but are generally of the uniserial ladder or unbroken cellular type (defined here as a continuous or near-continuous medulla with distinct cells; like a continuous ladder). These monkey hair medullae nearly all have irregular margins (scalloped, fringed, or angular). The medullae of bushbuck hair are continuous with straight margins, but they are also extremely broad (width exceeding 70% of the total hair diameter). The medullae of bushpig hairs are variably continuous and sometimes narrow, like the target hairs, however, the midshaft diameter of bushpig guard hairs (mean = $270.3 \mu\text{m}$) are over twice as large as the midshaft diameter of even the most massive target hair ($111.9 \mu\text{m}$). The mean midshaft

diameter of target hairs (mean = 75.3 μm) approximates that of immature chimpanzees (mean = 75.5 μm) but is markedly lower than the midshaft diameter of mature chimpanzees (mean = 108.4 μm). This supports the observation by H. Inagaki [in Bakuneeta et al., 1993] that young chimpanzees have thinner hairs than adults.

All target hairs have imbricate cuticle scales with a wave pattern and primarily rippled (though with some smooth) margins (Fig. 2). This is consistent with all chimpanzee hairs examined in this study and the findings of previous studies [Bakuneeta et al., 1993; Inagaki and Tsukahara, 1993]. The proximodistal distance between scale margins near the midshaft is narrow and also comparable between target hairs (mean = 6.0 μm) and chimpanzee hairs (mean = 6.3 μm). The cross-sectional shape of all target hairs is uniformly round along the shaft of the hair. Mature chimpanzee hair cross-sections are primarily oval in shape; however, immature hairs are mostly round. In humans, the hair of children tends to be rounder than in adults [Bogaty, 1969]. Accordingly, the round cross-sectional shape of the target hairs may potentially reflect the immaturity of the individual from which they came.

Fecal samples belonging to 8 Kasekela group mates of Fanni are all negative for hair of any kind. Of the 6 additional fecal samples collected from Fanni, only 1 (from August 3, 2007) contains hair, and only a single guard hair was recovered. This guard hair was reddish-brown, unbanded, and had a narrow uniserial ladder medulla, making it most consistent with red colobus hair.

Discussion

The results of this comparative hair morphological analysis strongly support the hypothesis that chimpanzee hairs can be differentiated from the hairs of their most common prey, that the target hairs belong to a (likely young) chimpanzee and that Fanni consumed said chimpanzee. Though there can be notable overlap in hair morphology between closely related taxa [Hess et al., 1985] and morphological variation according to body location [Stains, 1958; Knecht, 2012], only the hair of chimpanzees match the target hairs across all parameters. While 1 or 2 chimpanzee hairs may be found in chimpanzee feces due to grooming [Bakuneeta et al., 1993], no chimpanzee hairs were found in any of the 14 comparative fecal samples examined, and the relatively large number of hairs in the target sample, given the small quantity of excrement, is indicative of the consumption of chimpanzee tissue containing guard hairs. Moreover, the round shape and fineness of the target hairs is most consistent with the morphology of young chimpanzee guard hair.

It is important to note that though the group containing Fanni was described as excited on the morning of October 18, 2007, it is unlikely that the consumption of chimpanzee tissue occurred that day. The mean gastrointestinal tract transit time in adult chimpanzees is approximately 1 day (23.2 h [Lambert, 1997, 2002]). Fanni was part of a group followed by field assistants on October 16, 2007, from nest to nest, and she was not observed eating any meat that day. Accordingly, the incident probably occurred sometime on October 17, 2007.

It is impossible to determine the course of events that led to this cannibalistic event, but circumstantial evidence suggests that the cannibalism followed an infanticidal attack. Cannibalism by chimpanzees has only been observed in the aftermath of lethal attacks [e.g., Bygott, 1972; Goodall, 1986; Hamai et al., 1992; Watts and Mitani,

2000]. Chimpanzees rarely scavenge [Gilby et al., 2017] and have never been observed to scavenge conspecifics who have died of natural or accidental causes [Goodall, 1986]. Schweini's infant was the only individual that went missing in this time period across the 2 observed communities. All other chimpanzees were confirmed alive in the following days and there were no reports of intergroup interactions with the third monitored community. The characteristics of the presumed victim (newborn with a low-ranking mother) match all previously reported female-led infanticides in Gombe National Park [Goodall, 1977; Pusey et al., 2008]. Finally, Fanni was a known perpetrator in 2 previously observed [Pusey et al., 2008], and 1 subsequently observed [unpubl. data], infanticidal attack(s), and Schweini was acting fearfully when in her presence that day. Therefore, it seems likely that Fanni was involved in an infanticidal attack against Schweini. No other chimpanzee was observed with unusual feces that day, but given the incomplete tracking and fecal sample record, other chimpanzees may have been involved and/or consumed some of the carcass.

While genetic methods may ultimately be more accurate and may reliably identify the victim, they are not always feasible due to time, budget, and logistical constraints. Morphological hair analysis is a relatively inexpensive and quick method by which to coarsely identify chimpanzee hairs. The results of the present study suggest that the chimpanzee hair identification methods involving scanning electron microscopy utilized by previous studies [Bakuneeta et al., 1993; Inagaki and Tsukahara, 1993] are not necessary to differentiate chimpanzee hairs from the hairs of their most common prey. Size, color, banding, and medullae can all be reliably evaluated with a light microscope. Scanning electron microscopy does facilitate more accurate measures of scale dimensions, but general cuticle scale patterns can be observed equally well using casting methods. Lastly, while the study of hair cross-sectional shape cannot be easily undertaken outside of the lab or without sectioning equipment, any correlation between hair roundness and immaturity in chimpanzees remains anecdotal, and its value is debatable. Thus, overall, the most diagnostic information derived from guard hair in the present study was acquired using equipment that can be taken to the field and methods that can be performed there.

The simple methods employed in this study also show promise for the investigation of chimpanzee diet in general. While these methods cannot consistently differentiate among cercopithecine primates, they are useful for distinguishing colobines, cercopithecines, bushpig, and bushbuck (in addition to chimpanzees). With an expansion of the comparative hair sample to include rarer prey species, hair morphological analyses can be utilized to study the type of mammalian meat in chimpanzee diets. This is important because recent work suggests that females may specialize in easier to obtain prey items and may do so when solitary or in small groups, when they are less likely to be observed [Gilby et al., 2017]. Therefore, analysis of fecal remains for mammalian hair could elucidate the frequency and diversity of female hunting behavior.

Most importantly, our results indicate that morphological analysis of hair recovered from feces is a useful technique for the detection of cannibalism in chimpanzees and, thus, the likelihood that lethal aggression occurred. The rarity of lethal aggression limits our ability to investigate adaptive explanations for the behavior so the ability to increase sample size is likely to yield more fruitful investigations into the evolutionary basis of these behaviors.

Acknowledgments

We thank Tanzania National Parks, the Tanzanian Wildlife Research Institute, and the Tanzanian Council for Science and Technology for granting permission to conduct research for this project. We also thank Jane Goodall and the Jane Goodall Institute for funding and providing access to long-term research at the Gombe Stream Research Centre and the numerous field assistants who made behavioral observations and collected fecal samples under the direction of Shadrack Kamenya. We thank Thomas Gillespie for access to the fecal samples. We are grateful to Michelle Gignac (Duke University Shared Material Instrumentation Facility) and Mary Hutson (Duke University School of Medicine Histology and Microscopy Core Facility) for facilitating scanning electron microscope and microtome use, respectively. Doug Boyer and Mac Law graciously provided lab space and equipment for our work. We are also grateful to Nicole Edmison and the National Museum of Natural History for providing access to hair samples. Ian Gilby, Lindsey Cobb, Nichelle Reed, and Steven Churchill all provided valuable feedback on earlier drafts.

Disclosure Statement

The authors declare no conflicts of interest.

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