The Role of Diet in Self-Medication Among Chimpanzees in the Sonso and Kanyawara Communities, Uganda

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CHAPTER SEVEN

The Role of Diet in Self-Medication Among Chimpanzees in the Sonso and Kanyawara Communities, Uganda

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INTRODUCTION

With mounting evidence, the idea that primates obtain medicinal benefits from plant ingestion (e.g., Wrangham & Nishida, 1983; Huffman & Seifu, 1989; Wrangham & Goodall, 1989; Huffman *et al.*, 1993; Wrangham, 1995; Huffman, 1997; Huffman & Caton, 2001) is gaining acceptance among primatologists. The medicinal component of a plant is found in its secondary

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Primates of Western Uganda, edited by Nicholas E. Newton-Fisher, Hugh Notman, Vernon Reynolds, and James D. Paterson. Springer, New York, 2006.

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compounds, which taken in large doses are often toxic to most animals. They also reduce the palatability or digestibility of the plant. Scientists have discussed food selection according to the presence of secondary compounds in their diet and how animals cope with them while in search of food (Glander, 1975, 1982; Hladik, 1977a,b; Oates *et al.*, 1977, 1980; McKey, 1978; Milton, 1979; Wrangham & Waterman, 1981a,b). But it was Janzen (1978) who first suggested that animals' ingestion of plants rich in secondary compounds might actually help them fight pathogens and parasites. Subsequently, it was proposed that these compounds may also improve the reproductive fitness of an individual (Hart, 1990; Holmes & Zohar, 1990), and lessen the many diseases caused by parasites (cf. Allison, 1982; Toft *et al.*, 1991). Why primates ingest these secondary compounds has sparked interest in the fields of ethology, pharmacology, and parasitology, to name a few, and opened the door to the field of zoopharmacognosy (Rodriguez & Wrangham, 1992, 1993) also commonly referred to as primate self-medication (Huffman, in press).

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The term *zoopharmacognosy* was coined after evidence appeared supporting the idea that self-medication among primates existed. The basic argument is that animals exploit plant secondary compounds or other nonnutritive substances for curative purposes. In the field of primatology, chimpanzees have provided more evidence of self-medicative behaviors than any other primate species. Two types of self-medication behavior have been described in detail. One involves ingestion of an item rare to the diet and/or of little nutritional value (e.g., leaf swallowing, bitter pith chewing). Use of these plants tends to be restricted to certain seasons on the basis of reports to date, in particular when parasite reinfection is greatest. The individual ingests the plant item when infected with parasites and/or is showing related signs of illness (e.g., Huffman & Seifu, 1989; Wrangham, 1995; Huffman *et al.*, 1996). In some cases it has been shown that subsequent to the ingestion of the plant, the individual recovers from symptoms associated with the illness and/or expels the parasites in question (e.g., Huffman & Seifu, 1989; Huffman *et al.*, 1993, 1996). The second type of self-medicative behavior includes the ingestion of plants that are more common to the diet, but are also used ethnomedicinally or have demonstrated biological activity, suggesting a medicinal component. Huffman and colleagues (Huffman, 1997; Huffman *et al.*, 1998) proposed the term *medicinal foods*, borrowing the concept of food as medicine in traditional human societies (e.g., Etkin & Ross, 1982).

The following descriptions all fall into the first category of self-medicative behaviors. Whole leaf swallowing was the first such behavior reported by Wrangham (1975, 1977) and then later described in detail by Wrangham and Nishida (1983). These two researchers found folded, undigested leaves of *Aspilia mossambicensis* (Oliv.), *Aspilia pluriseta* (O. Hoffm.), and *Aspilia rudis* (Oliv. & Hiern) in chimpanzee feces at Gombe and Mahale. It was noted that the chimpanzees did not masticate the leaves but instead carefully placed them in their mouths one at a time, folding them with their tongue and palate and then swallowed them whole. This type of consumption suggested that ingestion of the leaves incurred no nutritional benefit, and so a medicinal or curative function was suspected (Wrangham & Nishida, 1983). Later, a phytochemical hypothesis based on the reported presence of thiarubrine A in *Aspilia* spp. leaves was proposed (Rodriguez *et al.*, 1985). Evidence for this hypothesis based solely on the presence of thiarubrine A in *Aspilia* spp. leaves providing strong nematocidal activity were not replicated by others (Huffman *et al.*, 1996, 1997; Page *et al.*, 1997). Moreover, cross-site comparisons of chimpanzees (Wrangham & Goodall, 1989; Huffman & Wrangham, 1994) and an extensive multiple ape species comparison (Huffman, 1997) revealed that many different plant species were being used in leaf swallowing by great apes across Africa. Huffman and colleagues (Huffman & Wrangham, 1994; Huffman *et al.*, 1996; Huffman, 1997) first realized that the leaves of all different species consumed in this manner have one peculiar trait in common: they are rough, and the surfaces are covered with bristly trichomes. At Mahale, a consistent pattern for the expulsion of parasites (the live adult worms of *Oesophagostomum stephanostomum*) along with leaves swallowed whole, was recognized by Huffman in the 1993–1994 rainy season at Mahale (Huffman *et al.*, 1996, 1997), while Wrangham at Kibale reported the relationship between the expulsion of proglottids of *Bertiella studeri* with whole leaf swallowing during a period of high tapeworm infection in 1993 (Wrangham, 1995). In addition, at Kibale, the chimpanzees swallow the rough leaves of *Rubia cordifolia* without chewing them: experiments conducted on different stages of nematodes from the genus *Strongyloides* showed that the leaves' extract had no effect on their motility, supporting the hypothesis of a physical effect via leaf-swallowing (Messner & Wrangham, 1996). On the basis of the observations, it was hypothesized that the leaves were consumed to flush the intestinal tract of nematodes or tapeworms, keeping infections at manageable levels (Huffman *et al.*, 1996). Leaf swallowing typically occurs in the

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early morning prior to eating or otherwise on an empty stomach (Wrangham & Nishida, 1983; Huffman *et al.*, 1997). A detailed analysis of the rapid time (6 h compared to the typical 30–40 h passage time) in which these unchewed leaves were passed through the gastrointestinal tract prompted Huffman and Caton (2001) to propose that consumption of these types of leaves on an empty stomach stimulate rapid gut motility, which flushes out the parasites.

A second example of this first type of self-medicative behavior was seen while following habituated chimpanzees in the Mahale Mountains. Huffman and Seifu (1989) opportunistically came across an adult female whom they observed to deliberately seek out and ingest the young pith of a tree, *Vernonia amygdalina*, commonly known as bitter-leaf. The chimpanzee bent down several shoots and meticulously stripped away the leaves and outer bark, revealing the inner pith, which she chewed and sucked for approximately 20 min. Further, detailed behavioral observations showed that she was unable to keep up with the group, lacked appetite, and her urine was darker than normal and stools were loose. Twenty hours after consumption, they were able to verify that she no longer showed any of these signs of illness from the previous day (Huffman & Seifu, 1989). A few years later, these observations were further supported by subsequent, more detailed observations of another female chimpanzee at Mahale (Huffman *et al.*, 1993). At this time, longitudinal parasitological studies were underway (Huffman *et al.*, 1997) and it was shown that, after ingesting the bitter pith of *V. amygdalina*, a significant drop in the parasite load of *Oesophagostomum stephanostomum* had occurred. This was accompanied by recovery from the visible symptoms of ill health (lack of appetite, malaise, diarrhea) within 24 h. In vitro the plant has demonstrated medicinal value, with activity noted against the parasites responsible for malaria, schistosomiasis, amebic dysentery, and leishmaniasis (Toubiana & Gaudemer, 1967; Kupchan *et al.*, 1969; Asaka *et al.*, 1977; Gasquet *et al.*, 1985; Jisaka *et al.*, 1992, 1993; Ohigashi *et al.*, 1994).

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Another putative self-medicative behavior seen in chimpanzees is the consumption of soils from termite mounds (Mahale, Gombe, Budongo) and from other specific places as natural holes and root masses of fallen trees (Kanyawara, Budongo). This behavior, called geophagy, was first shown in chimpanzees to provide low mineral intake compared to other chimpanzee food by Hladik and Gueguen (1974), and then suggested as a possible means of detoxifying secondary compounds present in the diet (Hladik, 1974, 1977a,b). Mahaney *et al.* (1996a,b) later suggested that soil consumption might also be beneficial remove Mahaney in press

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to individuals suffering from intestinal discomfort, for example associated with parasite infections. Mahaney *et al.* (1996a,b, 1997, in press) found that the soils consumed by chimpanzees in the Mahale Mountains and the Kibale Forest contain a type of clay comparable to kaolinite, not unlike Kaopectate™, a popular stomach medicine. Kaolinite can allay gastrointestinal upset, adsorb toxins and bacteria (Aufreiter *et al.*, 2001), and form a protective coating along the gastrointestinal tract (Johns, 1990; Mahaney *et al.*, 1996a,b, 1997; Stambolic-Robb, 1997). In addition, Ketch *et al.* (2001) demonstrated that the soils that chimpanzees selected for consumption were qualitatively different from other soils present in the chimpanzees' habitat. Soils selected by chimpanzees contained a higher proportion of soil microorganisms that produce antimicrobial and/or antiparasitic properties. One organism found was a filamentous bacteria (actinomycetes), which accounts for 75% of all known medicinal antibiotic compounds (Kutzner, 1981; Ketch, 2001). The second type of behavior can be illustrated by the consumption of a food item with interesting pharmacological significance such as the bitter-tasting berries of *Phytolacca dodecandra* or leaves of *Trichilia rubescens*. The Kanyawara group of chimpanzees at Kibale frequently eats these berries that are known to contain at least four toxic triterpenoid saponins (lemmatoxin, lemmatoxin-C, oleanoglycotoxin-A, phytolacca-dodecandra glycoside) capable of controlling schistosomes (Kloos & McCullough, 1987; Abbiw, 1990). The berries also possess antiviral, antibacterial, antifertility, spermicidal, and embryotoxic properties (Kloos & McCullough, 1987). In addition, compounds with highly significant in vitro antimalarial activity, trichirubines A and B, have been isolated and identified from *Trichilia rubescens* leaves, following the observation of unusual feeding behavior of Kanyawara chimpanzees: usually only one individual of the party selects and eats a few leaves from a young tree, even when more trees are present and available for itself and other individuals of the party (Krief *et al.*, 2004).

These are just a few examples of the potential health benefits from consuming plants with known medicinal properties already underlining the importance of comparing habits from different communities to highlight similarities and specificities related to potential local behavioral traditions in plant use. The aim of this chapter is to elucidate the potential medicinal value of dietary items consumed by the chimpanzees at two Ugandan sites, the Budongo Forest Reserve and Kibale National Park, and to discuss their possible roles in health maintenance. Demonstrating why chimpanzees consume the foods they do is difficult, but a solely nutritional role for foraging should not be assumed a priori. One way to identify and better understand the possible therapeutic benefits from plant ingestion is to document the foods consumed and the state of health of individuals before and after they consumed them. We review hereafter ethnomedicinal uses of plant parts eaten, which might provide interesting information from the empirical wisdom of indigenous people. A compilation of such data over a 9-month period in Budongo and a 5-month period in Kibale attempts to shed light on how the diet of chimpanzees might help to keep pathogens and parasites at manageable levels. We also preliminarily explore the possibility that even though the flora composition overlaps at these two sites, each community may have unique medicinal cultures.

METHODOLOGY

Study Sites

The Budongo Forest is approximately 428 km^2 and is described as a moist semi-deciduous tropical forest. Vegetation types include secondary mixed forest, swamp forest, and wooded grassland that lies between latitudes 1°35′–1°55′ N and longitudes 31°18′– 31°42′ E in the Bunyoro District of Western Uganda (Eggeling, 1947; Synnott, 1985; Plumptre, 1996). The Sonso community study site was established in 1990 by Vernon Reynolds and the Budongo Forest Project staff (Reynolds, 1992). The forest is drained by the Sonso and Waisoke rivers, which flow into Lake Albert. This study was carried out by PP from February to October 1998. During this time the total rainfall was 1845 mm. The rainiest months were April–May and September–October. Altitudes range from 910 to 1100 m above sea level. Mean annual minimum temperatures range from 17 to 20°C to maximum temperatures of 27–29°C.

The Kibale National Park covers 766 km^2 located in the Kabarole district of Western Uganda, between 0°13′–0°41′ N and 30°19′–30°22′ E. The area lies between an elevation of 1300 and 1500 m, and the rainfall averages 1700 mm per year. Vegetation of this midaltitude moist forest also includes secondary forest, grassland, swamp, Eucalyptus and pine plantations, and elements of lowland tropical rainforest. Mean daily temperatures range between 14.9 and 20.2°C and rainy seasons occur from March to May and from September to November (Chapman & Chapman, 2004). The study conducted in the Kibale Chimpanzee Project by SK comprised a 3-month period in the dry season (December–February 2001) and two 1-month periods in the rainy season

(October 2001 and October 2003) of observation of the Kanyawara community. Facilities at the study site of Kanyawara were provided by Makerere University Biological Station.

Fecal and Urine Analysis

In the field, urinalysis can be an important noninvasive tool available to researchers when monitoring the health status of an individual (Kaur & Huffman, 2004; Kelly *et al.*, 2004).

Sonso

A total of 299 fecal samples were collected primarily from 14 known adult individuals and stored in three preservatives when possible. Immediately after defecation, the fecal sample was examined macroscopically for presence of whole leaves and proglottids; the state of the feces (firm, soft, or diarrheic) was documented. A representative sample free from soil was then collected and stored individually in 5.0-ml sterile Corning™ vials. In camp, vials and feces were weighed and 1-g samples were fixed within 3 h of collection. The primary preservative was 10% neutral formalin; secondary preservatives were polyvinyl acetate and Proto-fix. The contents were mixed and stored in a cool dark room. The samples were later analyzed microscopically by Alpha Tec, Inc., and Dr. S. Gotoh at the Primate Research Institute, Kyoto University. Dr. Gotoh also measured parasitic load via the MGL (formalin ether sedimentation) and MacMaster techniques (expressed as eggs/g feces [EPG]). A few samples were examined on site by the MacMaster flotation method using zinc sulfate and direct examination. Owing to time constraints, expertise level, and field conditions, it was not possible to examine on site all samples collected.

Some parasites can be determined from microscopic examination; others, like *Oesophagostomum* eggs, are difficult to distinguish from hookworm eggs. Without expertise, the eggs need be cultured and examined at the larval stage, which is morphologically unique (Krepel, 1994). Twenty of the 299 samples were cultured using the Harada–Mori technique (Harada & Mori, 1955). Of these 20 samples, 10 were analyzed for the presence of *Oesophagostomum* by the laboratory of Prof. Ton Polderman and Coby Blotkamp from the Department of Parasitology, Leiden University, The Netherlands.

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Urine was analyzed opportunistically to detect potential illness. This was done using urinalysis reagent strips (Roche Chemstrip 9©) that tested the following parameters: glucose, bilirubin, ketones, specific gravity, blood, pH, protein, nitrites, and leukocytes. The urine was pipetted off the surface of leaves; it was never collected when possibly contaminated with feces or soil. The analysis was performed while in the field. A total of 15 samples were collected from 7 females and 3 males.

In humans, highly elevated levels of leukocytes may signal a urinary tract infection, kidney infection, cystitis, or urethritis (e.g., Pfaller *et al.*, 1987; Pezzlo, 1988). Normal levels range from 0 to 10 leu/μl. A pathological condition is thought to occur when levels are greater than 20 leu/μl.

Kanyawara

A total of 252 fecal samples from 38 known chimpanzees were collected, consisting of 187 samples collected during the dry season and 65 during the rainy season; 127 samples came from 18 females, and 125 samples came from 20 males. Methods are detailed in Krief *et al.* (2005a,b,c). They differed from those used in Sonso as MacMaster flotation was performed on fresh material, using $MgSO_4$. Two grams of each sample, stored in 18 ml of 10% formalin, were also analyzed by direct examination and diphasic ether–formalin concentration to search for rare eggs. Protozoan cysts were searched for in 0.5 g of feces fixed in merthiolate-iodo-formalin (MIF staining). Then, according to stool consistency, parasite loads as counted by the MacMaster method and direct examination were corrected by multiplying the count by a coefficient of 2 if the dung was soft and pasty and 3 if it was diarrheic or liquid (Hercberg *et al.*, 1986). These counts were called the "corrected parasite load."

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Fresh urine from chimpanzees in trees was collected either on the concave surface of a plastic bag or by pipetting the urine off the surface of leaves as described in Krief *et al.* (2005b). Urine samples, when not contaminated by feces or soil matter, were stored in a clean dry container and analyzed immediately on returning to the field station. The samples were tested with commercial dry reagent dipsticks (Multistix 10 SG Bayer©) for 10 parameters, including those listed for the Sonso community plus urobilinogen. The identity of the chimpanzee, date and hour of collection were noted. Urine obtained when the chimpanzee urinated from its night nest tends to be highly concentrated and is thus the most likely to be diagnostic of abnormality. Place and means of collection (e.g., leaf, pipeting, urine-stick use), amount collected, macroscopic aspects of urine such as color or turbidity, and presence of crystals were considered as potentially useful information. The analyses performed on 76 urine samples from 32 chimpanzees, including 45 samples (21 from males and 24 from females) collected during the dry season and 31 (13 from males and 18 from females) collected during the rainy season are described in Krief *et al.* (2005b).

Behavioral Observations and Plant Consumption

Sonso

The Sonso community comprised 52 individuals; of these, 14 adult chimpanzees were followed, 7 females and 7 males. Focal-animal and ad libitum behavioral observations were made. Chimpanzees were followed as long as possible from the time they left their night nests (352 h). The level of habituation at this time did not permit dawn-to-dusk follows. All behaviors were noted using a continual scan method. Health documentation included respiratory, digestive, reproductive, locomotive, and urine functions. Also documented were any signs of illness or injury, to include wounds, snare injuries, decreased appetite, sneezing, coughing, nasal or eye discharge, and level of activity (Huffman *et al.*, 1997). Fecal and urine samples were collected from known individuals whenever possible.

When documenting feeding activities, all plant and nonplant items consumed were noted and samples collected when possible; the location the feeding activity took place was also documented. A total of 33 plant items from 28 plant species were collected. Chimpanzees were also observed to feed on soil from termite mounds. Four samples were collected and sent for analysis to Mahaney and colleagues of the Geophagy Research Group at York University (see Tweheyo *et al.*, Chapter 8, this volume).

Kanyawara

The Kanyawara community of chimpanzees comprised 50 individuals, well habituated to the presence of the observers on the ground at a distance of 5–10 m. Chimpanzees have been monitored daily since 1987 by the Kibale Chimpanzee Project team directed by Richard Wrangham. In June 1999, 10 adult males, 2 adult females without offspring, and 14 mothers with 22 dependants (10 females and 10 males, 2 young infants of unidentified sex) were counted in the Kanyawara community.

Observations were conducted from dawn to dusk when possible. The focal subject was observed for a 10-min period to estimate activity budgets and diet.

The target was changed every 10 min whenever possible. During this study, 450 h of observations were collected in the dry season and 195 h during the wet season.

In addition, ad libitum observation allowed accurate recording of particular sequences related to possible self-medication. Attention was focused on the diet of the identified chimpanzees; all items ingested were recorded in detail. Veterinary work consisted of daily clinical observations (respiratory, digestive, reproductive, locomotive, and urinary functions), looking for clear signs of probable illness such as decreased appetite, long and frequent resting, sneezing, coughing, or intestinal disorder, as described by Huffman *et al.* (1997). Urinalysis and intestinal parasite evaluation were carried out. Whenever possible, feces and urine were collected from all known individuals.

RESULTS

Fecal Analysis

Sonso

During the study, 299 fecal samples were collected. Of these, 100 were analyzed by Alpha-Tec, Inc. These results are summarized in Table 1. They identified seven different species of helminthes: *Anoplocephala* (tentative identification) (12%), *Strongyloides* (65%), *Ternidens* (20%), *Necator* (49%), *Trichostrongylus* (2%), and two that could not be identified. One species of protozoa, *Troglodytella* (76%), was also found.

From the 44 samples analyzed by Gotoh, three parasite species were identified: *Strongyloides* (84%), *Oesophagostomum* (23%) and *Troglodytella* (93%). Among the 20 coprocultures prepared, 10 were analyzed by Polderman and Blotkamp. All contained *Oesophagostomum* third-stage larvae (L3) regardless of sex, age, or month the sample was collected. The samples identified as *Ternidens* by Alpha-Tec are most likely *Oesophagostomum*.

Kanyawara

During both dry and rainy seasons, the mean parasite count by direct examination was low (96% of the samples contained less than 1000 helminthes/g of feces), uniform and not significantly different (301 [$n = 187$] and 197 [n = 65], respectively, ns). These results are summarized in Table 1 and presented by Krief

Table 1. Summary of fecal and urinalysis for both communities

Parasite species	% Fecal samples infected: Kanyawara chimpanzees		% Fecal samples infected: Sonso chimpanzees		Abnormal urine value: Kanyawara chimpanzees	Abnormal urine value: Sonso chimpanzees
Method	MacMaster ($MgSO_4$)	DE	DE		Reagent strips	Reagent strips
No. of samples	239	247	144	No. of samples	76	15
No. of chimpanzees	38	38	14	No. of chimpanzees	32	11
Trichuris sp.	1.7	0.4		B	6	4
Strongyloides fulleborni	15.5	8.9	69	L	14	2
Oesophagostomum sp.	55	30.7	7	N	2	1
Probstmayria sp.	0.8	10.5		pH	2	
Necator americanus			49	P	1	
Ternidens deminutus			31	K	1	
Unidentified nematode	26.3	64	41	B & L	14	3
Bertiella studeri	0	2.8	12	B & N	3	1
Troglodytella abrassarti	0	66	80	L & N	2	1
Small entodiniomorphs	0	23		L & P	2	
				N & K	1	
				U & B	1	
				B, L, & N	1	1
				U, B, & N	1	1
				L, N, P, & G	1	

DE = direct examination; B = blood: G = glucose; K = ketones; L = leukocytes; N = nitrites; P = proteins; U = urobilinogen. Kanyawara data from Krief *et al.* (2005b).

et al. (2005b). Nevertheless almost all of the samples and the individuals were parasitized regardless of the method used. On the other hand, *Oesophagostomum* sp. and *Strongyloides fulleborni* were commonly observed and *Trichuris trichiura* and *Bertiella studeri* were rarely found (Krief *et al.*, 2003) as detected previously by Ashford *et al.* (2000). Among protozoa, two species of entodiniomorph ciliates were detected by direct examination: *Troglodytella abrassarti*, the more common protozoa, and a "small entodiniomorph," likely the same one described previously in studies in Kibale (Ashford *et al.*, 2000), Gombe (File *et al.*, 1976), Mt. Assirik (Mc Grew *et al.*, 1989) and La Lope (Landsoud-Soukate *et al.*, 1995).

Urine Analysis

Sonso

From August to October 1998, 15 urine samples were analyzed using a urinalysis reagent strip. These results are summarized in Table 1. This was not the primary objective of the study, and only a limited number of samples were obtained. Samples could only be collected when the chimpanzees were feeding low in the canopy as the urine was pipetted off the surface of leaves. Many samples had to be discarded as the fruits being consumed turned the urine bright yellow, causing the blank to fail. Of the samples analyzed, 13% gave a negative result for all nine parameters; both individuals were males. Forty percent of the samples, all from females, tested positive for leukocytes. Of those individuals that tested positive, only one had an activity budget that seemed abnormal. The sample obtained from KG on August 18, 1998, contained in excess of 500 leu/μl of urine. This chimpanzee slept more than 3 h in a 6-h focal; 1.5 h were spent grooming her son and the remaining time was spent feeding and moving only a short distance to obtain ripe fruits. Thirteen percent of the samples tested positive for nitrites. Only one chimpanzee had a urine pH of 7, all others had values of 8 or 9. One chimpanzee, KY, tested positive on 19 August 1998 for 3 parameters: leukocytes, nitrites, and hemoglobin. We estimate that this chimpanzee was approximately 4 months pregnant.

Kanyawara

As described in Krief *et al.* (2005b) leukocytes and blood were found respectively in 45 and 34% of the samples ($n = 76$) and were often associated together.

Fifty-three percent of the samples (cycling females excepted) had an abnormal value for at least one parameter. Half of the female samples were positive for blood versus 15% of the male samples ($P = 0.002$) but samples from noncycling females were also more often positive than samples from males ($P = 0.02$). Leukocytes were significantly more frequent in cycling females than in noncycling females. All but two urine samples had an alkaline pH (>7) (Table 1).

Plant Consumption

Sonso

From February to October 1998, the Sonso community of chimpanzees consumed 48 plant items from 41 plant species. Throughout the study period, fruits were the dominant food source consumed, with 21 species eaten corresponding to 58.5% of total times in the feeding budget; 10 species of leaves were consumed at 20.7%, seeds (two species) were ingested at 6.9%, and flowers (five species) at 3.6% (Table 2). *Ficus sur* fruits were so preferred during this study period that chimpanzees consumed them every month and at all stages of ripeness. Even during the month of October, when the figs were unripe, 16 observations were made of fruit consumption.

Kanyawara

Kanyawara chimpanzees consumed 46 plant items from 35 plant species during the study. Fruits were the dominant food consumed, with 19 species eaten corresponding to 81% of total time in the feeding budget. Leaves (16 species) were ingested at 15% and stems (seven species) at 3.5%. *Ficus natalensis* fruits were the most common food item in Kanyawara during the study period (Table 2).

Medicinal Plants Consumed

During the course of this study, the chimpanzees from both sites consumed a total of 69 different plants, all but 9 identified to species level (Table 2). Of these, 24 species are unique to Budongo, and 11 to Kibale, with 34 species found at both sites. Surprisingly, of the species present at both sites, the chimpanzees from both communities consumed only five items (14.7%) in common during this time period; the fruits of *F. sur* (= *capensis*), the leaves of *Ficus*

Table 2. Plants consumed by the Sonso and Kanyawara chimpanzees during the studies

Plant	Part ingested in Sonso	% of feeding time	Part ingested in Kanyawara	% of feeding time
Albizia grandibracteata			B[a]	
Acanthus pubescens	FL[a]	0.2	St[a]	2.1
Afromomum sp.	P	1.1	F, St	0.5
Alstonia boonei	B[a]	0.2		
Antiaris toxicaria	F	0.5	*L	<0.5
Balsamocitrus dawei	F	0.2		
Broussonetia papyrifera	L, FL	19.4		
Celtis africana			L	11.7
Celtis durandii	L[a]	0.3	F, L[a]	8.9
Celtis mildraedii	L	5.2		
Celtis wightii	L	1.3		
Celtis zenkeri	L	3.1		
Chaetacme aristata			F, L[a]	<0.5
Chrysophyllum albidum	F	0.5		
Chrysophyllum perpulchrum	F	0.2		
Chrysophyllum gorungosanum	F	0.2		
Cleistopholis patens	F	0.3		
Cordia abyssinica			F	12.6
Cordia africana			F	<0.5
Cordia millenii	F	0.3	F	1.5
Costus sp.	P[a]	0.2		
Crassocephalum bojeri			L[a]	<0.5
Cynometra alexandri	S, B[a]	7.3		
Despatsia dewevrei	F	1.1		
Dialium excelsum	F	0.2		
Ekebergia senegalensis	FL	0.2		
Epiphytes		0.2		
Eucalyptus sp.			B	<0.5
Ficus asperifolia			F, L, St	<0.5
Ficus barteri	F	0.3		
Ficus brachylepsis			F	13.1
Ficus cyathistipula			F, L	<0.5
Ficus dawei			F	11.2
Ficus exasperata	L[a], B	3.9	F, L[a]	2.2
Ficus mucuso	F	4.7		
Ficus natalensis			*F	18.4
Ficus ottonofoli			F	2.5
Ficus polita	F	0.2		
Ficus sansibarica	F	0.8		
Ficus saussureana	F	0.2		
Ficus stipulifera			F	1.7

change * to 'a'

Au: Indicate what this asterisk stands for.

Table 2. *(Continued)*

Plant	Part ingested in Sonso	% of feeding time	Part ingested in Kanyawara	% of feeding time
Ficus sur (= F. capensis)	F[a], B	33.8	F[a]	0.6
Ficus thoningii			F	
Ficus varifolia	L	0.5		
Illigera pentaphylla			F	0.6
Jasminum sp.			L	<0.5
Khaya anthotheca	B[a]	0.2		
Laciodiscus mildbraedii	L	0.6		
Lannea welwitschii	FL, F	0.2		
Lepistemon owariense			L	1.1
Marantocholoa sp.	P	0.3		
Markhamia platycalyx			B[a]	<0.5
Mildbraediodendron excelsum	F	3.1		
Milletia dura			L	<0.5
Milletia sp.	F	0.2		
Morus lacteal	F	0.3		
Myrianthus arboreus			F[a]	0.8
Myrianthus holstii	F	1.0		
Parnari excelsa			F	1.8
Pennisetum purpureum			St	<0.5
Phytolacca dodecandra			F[a]	<0.5
Piper umbellatum			St[a]	<0.5
Pseudospondias microcarpa	L	0.2		
Psychotria capensis			F	<0.5
Raphia farinifera	W	1.9		
Sterculia dawei	F	0.2		
Strombosia scheffleri			L[a]	<0.5
Termite mound soil		1.0		
Tree cabbage	L	1.1		
Trichilia rubescens			L[a]	<0.5
Triumfetta sp.			L	<0.5
Urera camaroonensis	S, FL	0.6		
Urera sp.			FL	3.6
Unidentified THV	P	0.3		
Unknown		2.6		

F = fruits; L = leaves; FL = flowers; P = pith; B = bark; W = wood; St = stems.
[a] Plants with ethnomedicinal properties. Unknown items were typically climbers that were too high to obtain a sample. In the case of THV, what remained after consumption was inadequate to positively identify.

exasperata, the pith of *Afromomum* sp., the leaves of *Celtis durandii* and the fruit of *Cordia millenii*. Both communities also consumed *Acanthus pubescens*, but different parts were ingested. It was the flowers at Budongo and the stems at Kibale. When the dietary items were expanded to include Newton-Fisher's 1994–1995 data, only two additional items were found to be common, the leaves of *Trichilia rubescens* and the pith of *Pennisetum purpureum* (Newton-Fisher, 1999a,b,c). It is interesting that of the seven items shared, six of them have ethnomedicinal uses, four of which (*F. exasperata*, *Afromomum* sp., *T. rubescens*, and *A. pubescens*) demonstrate bioactive properties.

Au: Delete whichever (a, b, or c) is inapplicable, in all citations throughout the chapter.

a, b, c must be Nick's addition. We only have one citation in our original text. Afr. J. Ecol. 37, 344–354.

If Nick thinks the other two are appropriate leave them.

Table 3 presents ethnomedicinal uses and pharmacological properties of the plants that were consumed at both sites during the study. The following behavioral and health-related observations were made in association with ingestion of these plants.

Observations from Budongo

Alstonia boonei bark. There are many ethnomedicinal uses for *Alstonia boonei*, including for diarrhea, nausea, worms, and stomachache. In addition, it possesses antimalarial, antiprotozoal, and antimetazoal properties (Table 3).

On May 5, 1998, at approximately 1700 h, four adult males traveled to a large *A. boonei* tree. They chewed the outer bark, then began to strip approximately 1/4 in of the outer bark away and consumed the inner bark. This continued for approximately 10 min. One member of the group, KK, an adult male, was followed that day for approximately 8.5 h. The majority of his time was spent foraging (44%), followed closely by resting (39%). No fecal sample was obtained from KK on the day of the focal, but one was collected the next morning that contained an anoplocephalid cestode [from direct laboratory examination, genus and species unknown] and the nematode *Necator*. Fecal samples were also collected from the other males who consumed the bark with KK. Samples from AY (April 28, 1998) and DN (April 27, 1998) both showed the presence of *Strongyloides fulleborni*, *Ternidens deminutus* and *Troglodytella abrassarti*. *Oesophagostomum* cultures were performed on three of the four males during the study (DN, AY, and NJ), and all tested positive for presence of this parasite.

Au: Add Ndayiwayeko & Ntungwanayo, 1978, to the list.

Remove 't' name is Nadayiwayeko

Ficus sur (= capensis) bark. Traditional medicine uses the bark of *Ficus sur* to treat bronchitis, dysentery, and stomach ache (Table 3).

Ndayitwayeko, A., & Ntungwanayo, V. (1978). Contribution à l'étude de plantes médicinales dans la région de Mugamba. (Commune Mugamba). Mémoire de licence, Univ. Burundi, Fac. Sc., p.129

Table 3. Medicinal plants consumed by the Sonso and Kanyawara chimpanzees

Family, Genus species	Ethnomedicinal uses for plant part ingested (source)	Pharmacological properties (source)	Part of plant consumed	Community that consumes
Acanthaceae, *Acanthus pubescens*	Dermatosis, sterility (1)	Antibiotic (3)	Flowers	Sonso
Acanthus pubescens	Abcess, skin disease (2)		Stems	Kanyawara
Apocynaceae, *Alstonia boonei*	Diarrhea and nausea (4, 5) Snakebites (4) Stomachache and malaria (5) Stomach worms (6) Worms (7, 8) Measles (9)	Antiprotozoal and Antimetazoal (7, 8)	Bark	Sonso
Asteraceae, *Crassocephalum bojeri*	Malaria, rhinitis, detoxicant (10) 3-day fever (11)	Antimalarial activity of aerial parts (12)	Leaves	Kanyawara
Commelinaceae, *Commelina* sp.	Child's fever (5) Medicinally (14) Tumor (15)	ND	Leaves	Sonso
Aneilema sp. (*A.aequinoctiale* for Kanyawara)	Rash (16)	ND	Leaves	Kanyawara Sonso
Euphorbiaceae, *Acalypha ornata*	Relief of postpartum pain (14)	ND	Leaves	Kanyawara
Gramineae, *Pennisetum purpureum*	Infammation of mammary glands (17) Anthelminthic and for amoebiasis (18)	ND	Stems, piths	Kanyawara and Sonso (Newton-Fisher, 1999a,b,c).
Leguminosae, *Albizia grandibracteata*	Antiparasitic (19) Swollen belly (20, 21)		Bark	Kanyawara and Sonso
Cynometra alexandri	Wounds (4) Acute backache (6)	ND	Bark	Sonso
Meliaceae *Khaya anthotheca*	Headaches (6) Parasites (22) Fever (23)	ND	Leaves	Sonso
Khaya anthotheca	Wounds (6)	ND	Bark	Sonso
Trichilia rubescens	Gonorrhea (24) Soporific, bruises, lumbago, dysentery, purgative (14)	Antimalarial (25)	Leaves	Kanyawara and Sonso (Newton-Fisher, 1999a,b,c)

(cont.)

indentation Snakebites, Stomachache and.., Stomach worms should be aligned with Diarrhea

Table 3. *(Continued)*

Family, Genus species	Ethnomedicinal uses for plant part ingested (source)	Pharmacological properties (source)	Part of plant consumed	Community that consumes
Moraceae *Ficus exasperata*	Diarrhea (6) Antiulcer remedy (26) Kidney complaints (4) Colic, cough (27)	Anthelminthic, Analgesic (14), Antinematodal and insecticidal (27, 28)	Leaves	Kanyawara and Sonso
Ficus mucuso	Analgesic, bronchitis, convulsions, otitis (29)	ND	Leaves and fruits	Kanyawara and Sonso
Ficus natalensis	Pains and venereal disease (30)	ND	Leaves and fruits	Kanyawara and Sonso
Ficus thonningii	Bronchitis and urinary tract infection (29, 31)	ND	Leaves and fruits	Kanyawara
Ficus sur (= *F.capensis*)	Bronchitis, dysentery, antidote (32)	ND	Bark	Kanyawara and Sonso
	Stomach disorders (5) Sterility (33) Laxative, abortifacient, aphrodisiac (34) Lactogenic, dermatosis (14)	text starting in caps are not to be indented	Fruits	Kanyawara and Sonso
Olacaceae *Strombosia scheffleri*	Abdominal complaints (13)		Leaves	Kanyawara
Phytolaccaceae *Phytolacca dodecandra*	Bilharziosis (35)	Triterpene saponins: molluscicidal, antiviral, antibacterial, spermicidal, antifertilizing activities (36, 37, 38)	Fruits	Kanyawara
Piperaceae *Piper capense*	External parasitism (39)	ND	Stems	Kanyawara
Piper umbellatum	Tonic (40)	ND	Stems	Kanyawara
Ulmaceae *Celtis durandii*	Cough and stomachache (6)	ND	Leaves and bark	Kanyawara and Sonso
Celtis africana	Indigestion (30)	NS	Leaves	Kanyawara

Table 3. *(Continued)*

Family, Genus species	Ethnomedicinal uses for plant part ingested (source)	Pharmacological properties (source)	Part of plant consumed	Community that consumes
Chaetacme aristata	Back wounds and spinal weakness (6) Antituberculosis (41)	Bacteriostatic (42)	Leaves	Kanyawara
Urticaceae *Myrianthus arboreus*	Hypoglycemic, analgesic, bronchitis, help to give birth (24)		Stems	Kanyawara
Myrianthus arboreus	Dysentery (43) Toothaches, bronchitis (44)	Triterpene acids (43) Triterpenoid (44)	Leaves	Kanyawara
Myrianthus arboreus	Emetic, purgative (24)		Fruits	Kanyawara

ND = No data; NS = Not significant; Sources: 1. Baerts & Lehmann (1991); 2. Ndayiwayeko & Ntungwanayo (1978); 3. Krief (2005a); 4. Terashima *et al.* (1991); 5. Ichikawa (AFLORA) (1998); 6. Howard *et al.* (1991); 7. Thomas & Mbenkum (1987); 8. Davies & Richards (1991); 9. Falconer (1991); 10. Kokwaro (1976); 11. Nyakabwa & Gapusi (1990); 12. Weenen *et al.* (1990); 13. Terashima *et al.* (1992); 14. Watt & Breyer-Brandwijk (1962); 15. Hartwell (1967/1971); 16. Altschul (1973); 17. Kayonga & Habiyaremye (1987); 18. Sugiyama & Koman (1992); 19. Balagizi Karhagomba, & Ntumba Kayembe (1998); 20. Defour (1994); 21. Heine & König (1988); 22. Jeanrenaud (1991); 23. Uphof (1968); 24. Bouquet (1969); 25. Krief *et al.* (2004); 26. Akah *et al.* (1998); 27. Abbiw (1990); 28. Ohigashi *et al.* (1991); 29. Bouquet *et al.* (1971); 30. Kokwaro (1976); 31. Iwu (1993); 32. Ayensu (1978); 33. Ake-Assi (1992); 34. Bouquet & Debray (1974); 35. Mesfin & Obsa (1994); 36. Taniguchi *et al.* (1978); 37. Kloos & McCullough (1987); 38. Katende *et al.* (1995); 39. van Puyvelde *et al.* (1985); 40. Polygenis-Bigendako (1990); 41. Ake-Assi *et al.* (1981); 42. Krief *et al.* (in press); 43. Ojinnaka *et al.* (1980); 44. Ngounou *et al.* (1988).

Au: Add ake-Assi *et al.*, 1981 to the refence list.

Consumption of *F. sur* bark was observed on two occasions. The first observation was made May 4, 1998, at 1440 h. Several chimpanzees were found on the ground biting off bark from the buttresses, and the inner bark was stripped away. The bark was then chewed. After several minutes the resultant wadge was discarded. On this day the chimpanzees were also eating unripe fruits of *F. sur*. The second observation occurred May 11, 1998, at approximately 1500 h. An adolescent female, SH, was found feeding on the bark. It was consumed in the same manner as described above. Both observations were ad libitum, and no further behavioral or fecal data were collected.

Ake-Assi,Y.A. (1992). Contribution au recensement des espèces végétales utilisées traditionnellement sur le plan zootechnique et vétérinaire en Afrique de l’Ouest. Thèse de doctorat (Sc. Vétérinaires), Lyon, Université Claude Bernard, 220 p.

Khaya anthotheca bark. Ethnomedicinally, the bark from *Khaya anthotheca* is used to treat parasites, aid in the healing of wounds, and for fever (Table 3).

On October 3, 1998, GS, a subadult male, was seen feeding on the bark of *K. anthotheca*. The observation was made at 0913 h. No record of this individual's parasite burden was collected at the time.

Observations from Kanyawara

Albizia grandibracteata bark. This is traditionally ingested as a medicine in Uganda and in the Democratic Republic of Congo (DRC) against intestinal parasites and bloat (Heine & König, 1988; Defour, 1994). Bioactive saponins have been extracted and isolated from leaves of this species (Krief *et al.*, 2005a,b,c) as well as from bark (Krief *et al.*, in press).

Au: Please update this in press artile, if possible.

On October 16–20, 2001, OK, a 6-year-old female, was observed to be suffering from intestinal disorder. The diagnosis was based on alternately dry, soft, and liquid stools. In addition, fecal analysis revealed a high load of parasitic infection (strongyle species and *Probstmayria gombensis*) (Krief, 2004). We observed OK eating *Chaetacme aristata* leaves on October 16, 2001, *Albizia grandibracteata* bark at 0942 h on October 20, 2001, and *Myrianthus arboreus* stems on October 22, 2001. In these three cases, she was the only chimpanzee of the party to consume the items. This was also the first recorded time since the observations began in Kanyawara in 1987 that a chimpanzee had been seen to consume the bark of *A. grandibracteata*. She ate it for 3 min while her mother and siblings were waiting for her. Feces collected October 22 had a normal consistency and the parasitic load was nil. *A. grandibracteata*, *C. aristata*, and *M. arboreus* are used in ethnomedicine (Table 3). This observation raises the possibility that OK's bark eating associated with ingestion of other specific items were responsible for reducing the high parasite load and alleviating digestive symptoms seen since October 16.

Phytolacca dodecandra fruit. This item is known for its antiparasite bioactivities as described in the Introduction and is considered to be toxic by the traditional healer of Kanyawara. Consumption was observed for three individuals (KK, LK, and NS) of a large party on October 29, 2003.

Trichilia rubescens leaves. Bioassays revealed a strong antimalarial activity of the leaf extract and led to the isolation of two new limonoids having an

IC_{50} on *Plasmodium falciparum* in culture roughly equivalent to chloroquine (Krief *et al.*, 2004). Kanyawara chimpanzees feed only occasionally and in short bouts (3 to 7 min for our five observations) on *Trichilia rubescens* leaves. For each observation, only one chimpanzee ate a few leaves (ca. 5/min) in each bout, whereas this individual was always included in a party of several individuals who were resting, feeding, or traveling. Four fecal samples collected from KK on February 2, 2001, a day when he was observed ingesting *T. rubescens* leaves, contained all helminthes larvae or eggs. Of the four samples collected in the three following days, only one was positive, with one *Trichuris trichiura* egg.

Piper capense stems. Stems of this species are used as an antiparasite in traditional medicine (Table 3). TU was observed consuming the stems of this item, which is an uncommon food in Kanyawara (February 16, 2001). A fecal sample was collected the same day and analyzed (MacMaster method), revealing seven *Oesophagostomum* eggs. A sample analyzed from February 20, 2001, was negative.

This item was also consumed by BB along with *Pennisetum purpureum* stems (February 15, 2001). Fecal samples collected prior to consumption contained *Oesophagostomum* sp. (February 14, 2001, MacMaster) and *Strongyloides fulleborni* (February 15, 2001, MacMaster).

In Both the Sonso and Kanyawara Communities

Celtis durandii leaves. These leaves are used ethnomedicinally for coughs, stomach ache, and edema from trypanosomiasis, back wounds, spinal weakness, and antituberculosis. Bacteriostatic properties are also present.

Sonso: On May 9, 1998, focal observations were made on KL, an adult female. Duration of the focal observation was approximately 3 h 30 min. The majority of the time was spent foraging (50%), followed by resting (26%) and grooming her infant (18%). Between 0926 h and 1001 h, KL was seen feeding on young *C. durandii* leaves. A fecal sample taken that day contained eggs of *S. fulleborni* and *T. abrassarti*.

Ficus exasperata leaves. These leaves are used in traditional medicine for diarrhea, as an ulcer remedy, for kidney complaints, colic, and cough. Antihelminthic, analgesic, and insecticidal properties are known.

Sonso: The mature leaves are usually not consumed, as the surface of the leaf is rough. One ad libitum observation was made of the mature leaves of *F. exasperata* being consumed. On August 13, 1998, ZT began to pick 4+ leaves at a time. He bit off the stems, rolled the leaves up, bit them in half, chewed, and then consumed the remaining half. This behavior lasted approximately 12 min. A fecal sample taken at the time contained *T. abrassarti* and *Oesophagostomum* sp.

Kanyawara: On February 15, 2001, a fight was observed between two adult males, YB and LB. YB bit LB's foot. The fifth toe was severely cut, hanging from his foot by only a strip of skin. Leaves and stems of *F. exasperata* were the only unusual food consumed in the following days.

Ficus sur (= capensis) immature fruits. Uses include a treatment for sterility, a laxative, abortifacient, or aphrodisiac, and have known lactogenic and antidermatosis properties.

Sonso: Consumption of immature *F. sur* fruit is common.

Au: Which year was this data recorded?

Kanyawara: On February 15, a 17-year-old male, KK, was weak and had a deep cough. Sneezing was frequent and analysis of his feces showed a large number of *P. gombensis* (1750 parasites/g) and was positive for strongyle eggs and larvae and *Trichuris* eggs. The activity budget of KK when compared to 13 other individuals from the same party shows that KK rested 77% of the time (compared to 33% for the rest of the group) and fed during only 16% of the time (compared to 48% for the other individuals). KK was the only individual from the party to feed on immature figs from *F. sur*, which are usually consumed only when mature. Urinalysis on February 15 revealed a low pH value.

February 15, 2001

Commelinaceae leaves. Chimpanzees at Budongo and Kanyawara are known to swallow leaves whole from the Commelinaceae family (C. Bakuneeta, V. Reynolds, personal communication, for Budongo; Messner & Wrangham, 1996, for Kibale). However, no personal observations were made during the study period. Unchewed leaves from the genus *Commelina* or *Aneilema* were found twice in the dung. The first instance was an ad libitum observation on May 16, 1998, of the adult male VN. In addition to the presence of adult worms on the surface of the leaf, microscopic examination detected *S. fulleborni* and *T. abrassarti*. The second time whole leaves were found was also an ad libitum observation on June 24, 1998, from an adult female, KL. No adult worms were detected; the fecal sample collected did contain *T. abrassarti*.

Soil Consumption

Sonso

A detailed report of the soil analysis from Budongo can be found in Chapter 8 of this volume. Ingestion of termite mound soil was recorded six times by five individuals during the study period. Of these six cases, two were recorded during focal-animal observations.

On August 22, 1998, the adult female KY, approximately 4 months pregnant, ingested soil at 1125 h. She spent the majority of this 10-h focal observation foraging (52%), followed by resting (28%) and moving (14%). Two fecal samples were obtained that day. The first specimen taken at 0655 h detected no parasites. The second taken at 1602 h contained *T. abrassarti*. On August 25, three days later, this same chimpanzee was seen eating soil at 0912 h (ad libitum observation). Neither behavioral data nor fecal analyses are available for this day.

On August 27, 1998, the adult female KW and her infant son KZ were observed sharing soil at 0856 h. After the mother began to consume the soil, the infant placed his hand near her mouth and requested soil from her. Initially she pushed some soil out from her mouth, which he took and placed in his mouth. When subsequent requests were made, she broke off a small piece from a larger piece and handed it to him. This interaction lasted approximately 9 min. An overwhelming amount of time from this 255-min focal was spent foraging (93%). The remaining time was spent moving (3%) and resting (4%).

Three fecal samples were collected from KW: one on August 19, one on August 25, and another on August 27, 1998, the day geophagy took place. All showed the presence of *T. abrassarti*. Two of the three samples contained *Oesophagostomum* sp.

Kanyawara

Geophagy was observed three times during the study period. In all cases, two individuals were eating soil. In each case, one of the two individuals had eaten *Myrianthus arboreus* before this. In two cases, fruits (ripe or immature) and young leaves on one occasion were ingested before this.

On December 22, 2000, ingestion by the old female LP, who was suffering from bloat and abdominal distension, was observed. Moreover, her hand was in pain, and could not be used for tree climbing. She built her nest early (1720 h) in spite of the feeding activity of the other individuals. The following day, she went out of her nest at 0750 h, which was late compared to her offspring, who had climbed down from the tree at 0700 h.

In the beginning of February 2001, this old female exhibited concomitant abnormal urinalysis (proteins and leukocytes), coccidiosis, and a high parasitic load. On February 5 at 1405 h and 1415 h, she was observed rummaging through fresh elephant dung, removing, crunching, and swallowing unidentified seeds from it. At 1540 h, she ate soil for 2 min. Five days later, at 0950 for 5 min, she ate several handfuls of fine fibrous material from an old fallen hollow trunk. A dung sample from this day was soft and contained high amounts of *T. abrassarti* (about 32,000/g) (Krief *et al.*, 2005b).

DISCUSSION

During the two study periods, the chimpanzees of both communities consumed 24 plant species used in traditional medicine. Of them, eight species possess known pharmacological properties (Table 3) that could have aided in the medicinal treatment for some of the symptoms or illnesses identified in the particular chimpanzees at the time of ingestion. They include *Acanthus pubescens* stems and flowers, *Alstonia boonei* bark, *Crassocephalum bojeri* leaves, *Albizia grandibracteata* bark, *Ficus exasperata* leaves, *Phytolacca dodecandra* fruit, *Trichilia rubescens* leaves, and *Chaetacme aristata* leaves.

The consumption of these eight plants was looked at in detail. Behavioral observations and fecal and urine analysis were used to gain insight into the individual's state of health at the time that the plant in question was ingested. Only the consumption of *A. grandibracteata* bark fits the first type of self-medicative behavior described by Huffman (1997). Although they possess bioactive properties, the remaining plants appear to fall into the second type of self-medicative behavior, which use "food as medicine" (see Huffman, 1997, 2003), with a special place to *T. rubescens* leaves because the low amount consumed and the high bioactivity do not really fit with a "food" category. These plants contain secondary compounds, which could play a role in health maintenance. All are food items rare to the diet. One curious aspect is that many times, only a few individuals in the groups ate these plants while others ignored or looked on. In addition, in the case of *Acanthus pubescens* flowers, a plant that possesses in vitro antibacterial properties, the chimpanzees were food grunting, so taste appeared to reinforce their consumption of this item. The difference between food and medicine is often difficult to detect even in humans. The concept of medicinal foods introduced by Etkin and Ross (1982) is supported by Johns (1990), who believes these nonnutritional components, once part of our diet, have now been replaced with herbal medicine and modern pharmaceuticals. Within traditional human societies worldwide, there is much overlap between food and medicinal items. The preliminary observations of our study further suggest this to be true for chimpanzees as well. Owing to secondary compounds present in some of these infrequently ingested plants, the medicinal value of these plants may exceed their nutritional value (Huffman, 2003). Observations recorded in this study that fit this second type of self-medicative behavior include *A. pubescens* stems and flowers, *A. boonei* bark, *P. dodecandra* berries, and the leaves of *C. bojeri*, *T. rubescens*, *Strombosia scheffleri*, and *C. aristata*. While we cannot quantitatively assess the underlying motivation for consumption, on the basis of our observations of health at the time of ingestion in some cases, it can be concluded that the individuals were possibly ill. Future research should search for pharmacological properties in the remaining 16 plants found in their diet that are known to be used ethnomedicinally.

Soil may have also provided medicinal benefits. Analyses of the soils consumed at Budongo and in Kibale strengthen the argument of consumption to alleviate gastrointestinal distress, suppress diarrhea, or possibly as a detoxification agent as the samples all contained clay similar to Kaopectate^{TM}. The first two observations of geophagy in Budongo occurred 3 days apart. There were times during the study when diarrhea was prevalent on the trails, and it was usually found in association with the consumption of unripe *F. sur* fruits. At this time the chimpanzees were eating the leaves, ripe fruits, and flowers of *B. papyrifera*, the ripe fruits of *F. sur*, and the seeds of *Urera camaroonesis*. The chimpanzee that consumed the soils was then 4 months pregnant. We do not believe chimpanzees experience nausea and gastrointestinal distress associated with pregnancy (Dr. Rick Lee, personnel communication), but the clay present in the soils could have decreased the levels of metabolic toxins such as steroidal metabolites associated with pregnancy (Johns & Duquette, 1991). Another possibility is that her parasite burden was higher than normal. In humans, pregnant and lactating females may be immunologically compromised and thus more susceptible to parasite infection (Kalema, 1995a,b).

Au: Delete whichever (a or b) inapplicable.

remove b from here. We only have one report: Kalema, G. (1995). A survey of intestinal parasites of a community of wild chimps, Pan troglodytes in the Budongo Forest, Uganda. Unpublished.

Kalema felt this was a contributing factor in higher egg counts of fecal parasites in females than males in a Ugandan population of mountain gorillas. The next observation discussed was a mother and infant sharing soil. The mother had *Oesophagostomum* and a large number of *T. abrassarti* eggs present in two fecal samples surrounding the consumption of soil. *T. abrassarti* is believed to be a symbiont that aids in the digestion of cellulose. Fluctuation in numbers is likely to be related to corresponding changes in dietary fiber intake. The soils consumed by the Kanyawara chimpanzees during this study were not analyzed, but analysis from previous studies at Kibale (Mahaney *et al.*, 1997, in press) showed it to be similar in composition to those analyzed at Mahale and Budongo (Mahaney *et al.*, 1996; Tweheyo *et al.*, Chapter 8, this volume).

The differences in plants selected seem pronounced between these two communities with regards to species with potential phytochemical benefits for maintaining health. Although there are many food plants shared in common between the two sites, which are separated by only 200 km (Chapman & Chapman, 2004), they exploited different plants with medicinal properties. Twenty-three percent of the 117 food species corresponding to 35 items ingested by Kanyawara chimpanzees are used in traditional medicine (Krief *et al.*, 2005a). Even when they consumed the same plant, the frequency of consumption varied as well as the part eaten. An example is *A. pubescens.* At Budongo the chimpanzees ate the flowers, which contain important antihelminthic and antibiotic properties (Krief *et al.*, 2005a) (Table 2) but no other part of the plant was consumed. Even when the flowers were present, the chimpanzees at Kibale ate only the stems.

Variation in the consumption of barks used in traditional medicine is another difference that exists between the Sonso and Kanyawara chimpanzees. It is a nonseasonal item, so availability is not an issue. During this study, the Sonso community consumed bark from five species of trees. Three of the five species (*F. sur*, *F. exasperata*, and *Cynometra alexandri*) exist at Kibale, however they were not eaten by the Kanyawara chimpanzees during this study nor has Wrangham ever observed their consumption at Kibale (unpublished data). Alternatively, during the study at Kibale, the bark of *A. grandibracteata* and *Markhamia platycalyx* was consumed. Both of these species exist at Budongo, but they were not eaten during the 1998 study period, nor during Newton-Fisher's 1994–1995 study (Newton-Fisher, 1999a,b,c). The possible role these barks play in health maintenance is unknown. Future research in the area of bark consumption and its underlying motivation is needed. But for *A. grandibracteata*, the potential role in health maintenance has been evidenced by bioactive properties against helminthes. Furthermore, the parasite levels of the individual that ate the bark of this species abruptly dropped after its consumption.

Goodall (1986) felt that variation in dietary items between sites was primarily due to food availability. Our analysis found that between Kibale and Budongo, 58% of all dietary items consumed during our studies are present at both sites. However, of these items only 8.45% were commonly consumed at both sites. In this case, availability alone cannot explain the differences we found. Wrangham offered another theory for intersite variation in diet. He believes that important differences may exist in plant chemistry (Goodall, 1986). Goodall offered a third hypothesis, which suggested differences are due to different group feeding traditions (1986). We suggest that both tradition and difference in plant chemistry may play a role in the unique "medicinal culture" found at each site. Future studies conducted in parallel are warranted to confirm the presence of secondary compounds and the amounts of each compound detected across sites.

In addition, it is plausible that regional differences in health status brought about by variability in parasites, pathogens, and other causes of illness could shape the different "medicinal cultures" among sites. We suggest that future studies looking for intersite variation perform both the MacMaster and direct examination methods of parasite detection. Given the demonstrated importance of *Oesophagostomum* as potential motivation for self-medication at some sites (Huffman *et al.*, 1996; Dupain *et al.*, 2002), knowing its prevalence and intensity of infection is important. Repeated infections can cause significant complications such as secondary bacterial infections, diarrhea, severe abdominal pain, weight loss, and weakness, which can result in high mortality (Brack, 1987). Therefore, we also recommend Harada–Mori coprocultures be performed. The combined impact of multiple-species infections needs to be looked at in more detail. Besides parasitological methods, fecal samples may also be used to look for fecal antigens and antibodies using molecular techniques (PCR) to aid in identifying a variety of pathogens responsible for disease. In addition to such noninvasive methods, we emphasize the necessity of knowing the etiology of death. Sick chimpanzees have to be followed carefully to find the carcass if the disease is lethal. Results of a necropsy may enable us to associate the real cause of death with the behavioral, fecal, and urine analysis from when it was alive. Urine analysis also provided insights into potential health problems. The sample size for the Sonso community is small, but the Kanyawara study was able to draw several conclusions based on their results. We would also advise Budongo researchers to implement periodic pregnancy testing of cycling females, a practice that already exists at Kibale. During the Budongo study, two positive pregnancy tests were obtained. Once a positive pregnancy test was recorded, careful monitoring of these chimpanzees took place, providing insight into behavioral changes associated with pregnancy and allowing the field assistants the opportunity to view one of the births (Kiwede, 1999).

In conclusion, our results suggested that unique medicinal cultures might exist at each of the sites in question. These two communities exploited different plants, different parts of the same plant, with varied degrees of frequency. We suggest future research continue to analyze dietary items to look for secondary compounds useful in health maintenance. Obvious illness is difficult to observe, so further research must focus on the chimpanzees' ongoing efforts toward consuming items that help it reach and maintain health homeostasis. Potential health problems can be detected by behavioral observation, fecal and urine analyses. Future research of this type may also lead to the discovery of new medicinal compounds for human medicine and help to explore questions regarding hitherto little explored aspects of primate medicinal culture.

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CHAPTER EIGHT

Geophagy in Chimpanzees (*Pan troglodytes schweinfurthii*) of the Budongo Forest Reserve, Uganda

A Multidisciplinary Study

change order:
Tweheyo Mnason

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INTRODUCTION

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Geophagy occurs widely among primate species (Krishnamani & Mahaney, 2000). While reported for chimpanzees in the wild since the 1960s (Hladik, 1977a,b; Nishida & Uehara, 1983; Goodall, 1986), the geochemical and behavioral study of geophagy in relation to self-medication (Huffman, 1997) was not initiated until the mid-1990s, the first being that of Mahaney and Huffman. This work began in Tanzania with the analysis of termite mound soils, behavioral and parasitological data collected from the Mahale Mountains National Park (Mahaney *et al.*, 1996a,b; 1998; Aufreiter *et al.*, 2001; Ketch *et al.*, 2001). Further analyses have included termite soils eaten by chimpanzees in Gombe National Park, Tanzania, and exposed subsurface clays eaten by chimpanzees in the Kibale National Park, Uganda (Mahaney *et al.*, 1997, 1998; Aufreiter *et al.*, 2001). Geophagy has recently been noted to occur in a fourth East African population, the Sonso community in the Budongo Forest Reserve, Western Uganda. Early published studies from Budongo did not report any kind of soil eating by chimpanzees. However, more recently, Reynolds *et al.* (1998) referred to the eating of riverbank soil and other authors have noted sporadic termite mound soil eating by chimpanzees in this forest (e.g., D. Quiatt in Reynolds *et al.,* 1998:335; Newton-Fisher, 1999a,b). Termite mounds of the species *Cubitermes speciosus* are present in the Budongo forest (Newton-Fisher, 1999b).

At Gombe, chimpanzees consume *Macrotermes* with the aid of termite fishing tools inserted in a mound's ventilation ducts (Goodall, 1986). Reference is made to the consumption of mound soils of *Pseudacanthotermes spiniger* in Mahale, as being distinct from the consumption of termite mound soil there (Uehara, 1982). In the case of *Cubitermes* at Budongo, however, chimpanzees consume termites along with lumps of earth wrenched from termite mounds. While information exists on the consumption of termites, little consideration is given to the depth reached by termite species. Pomeroy (1976) cites *Pseudacanthotermes* as a builder of smaller mounds in Uganda. *Cubitermes humiverus* is also a builder of small mounds that are characteristically mushroom-shaped. This species' shallow activity in the soil, unlike the other mound builders, is likely to produce high organic contents in mound soils, a characteristic antithetic to geophagy. Furthermore, nowhere is there a detailed analysis of soils that provides information on the different structural components of these mounds. When considering the ingestion of termite mound soils, this information is important for increasing our understanding of their selection by chimpanzees.

A central theme has been to explain geophagic behavior from the perspective of the ingested soils' physical, chemical, and mineralogical properties. Theoretically, there should be a common adaptive property or properties of the soil being selected for by primates that helps explain why they spend considerable time searching for and ingesting soil, sometimes on nearly a daily basis (e.g., Goodall, 1986; Mahaney *et al.*, 1998; Wakibara *et al.*, 2001). Previous work has drawn attention to the high percentage of clay in every instance of geophagy studied among chimpanzees (Wrangham, 1977; Mahaney *et al.*, 1996a,b, 1998), gorillas (Mahaney *et al.*, 1990, 1995a; Mahaney, 1993), orangutans (Mahaney *et al.*, 1996a), and macaques (Mahaney *et al.*, 1993, 1995b; Wakibara *et al.*, 2001). In addition, the clay mineral components have a near-perfect crystallinity in almost every detailed analysis carried out on these samples by Mahaney and colleagues of the Geophagy Research Group at York University. All the soil samples they have analyzed to date, they have identified a pharmaceutical-grade clay mineral of low Si composition (Si:Al = 1:1) belonging to the kaolinite, halloysite, and metahalloysite group.

Typo: In all the soil samples....

It has been suggested that the ingestion of small quantities of clay-rich earth may assist in nutrition, serve as a dietary supplement, or even have pharmaceutical properties beneficial to chimpanzees (Mahaney *et al.*, 1999; Aufreiter *et al.*, 2001; Ketch *et al.*, 2001; Mahaney & Krishnamani, 2003). Behavioral studies have yet to be fully incorporated into the research program, in part because of the rarity of occurrence of the behavior at some of these sites. The behavior is short in duration, hard to predict when it will occur, and thus difficult to sample completely. This paper reports the first attempt at Budongo to analyze the physicochemistry and mineralogy of soils eaten by chimpanzees and presents behavioral, dietary, and parasitological data in an attempt to assess the possible benefits of geophagy for chimpanzees at this site.

METHODOLOGY

The Study Site

Behavioral and chemical analyses presented here are from data and samples collected while pursuing other behavioral and ecological studies in the Budongo Forest Reserve of Western Uganda. The chimpanzees observed were members of the Sonso community, which has been investigated since 1990 under the direction of Vernon Reynolds. The Budongo Forest Reserve is a medium-altitude, Au: Note the change of Howard, 1991, to Howard *et al.*, 1991.

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moist, semideciduous forest, a mixture of tropical high forest with a large population of mahoganies, woodland, and savannah grassland (Eggeling, 1947; Reynolds & Reynolds, 1965; Howard *et al.*, 1991). The mean annual rainfall is 1780–1900 mm, with a short dry season from mid-December to mid-February. The mean monthly minimum and maximum temperatures are 17–20°C and 27–29°C, respectively (Newton-Fisher, 1999a,b,c; Tweheyo, 2003). Mnason, 2003

Field Protocols

The detailed behavioral observations and soil samples we analyze here were collected during two research periods. Period I in 1998 covers the period between February 23 and October 14, 1998. During this period, PP conducted behavioral observations using ad libitum and focal-animal sampling. In this period, we recorded all social interactions, activity patterns, diet, and visible cues of health status. We observed seven adult males and seven adult females for a total of 352 h over 105 observation sessions. We used these data to evaluate possible relationships between health status and geophagy. We also used this focal data to analyze for possible changes in diet around the months in which we observed geophagy. Additional ad libitum records of geophagy made by field assistants and other researchers are included in the general analysis and discussion, but not in calculations of relative frequency or diet involving total hours of observation.

Period II covers the period between June 10, 2000, and August 24, 2001, and was conducted by MT and field assistant Monday Gideon Mbotella for a total of 286 observation days per person, for a total of 572 h. Three days a week we used scan sampling, and 2 days a week we used focal sampling. From the 54-member community, a total of 34 (16 males, 18 females) adult and juvenile members in the group were observed. Focal sampling was done from dawn to dusk on one specific chimpanzee per day. Scan sampling was used to record chimpanzee diet, behavioral activities, and habitat use. Among juveniles and adults, both sexes were equally considered. Over a period of 176 days, 2641 scans were recorded, 2107 of which involved feeding. Period II focused on the food sources and abundance and ecology of food trees fed on by adult chimpanzees in the Sonso community.

Observations of geophagy made by project field assistants during the course of their daily observations after the completion of MT's study in early October 2001 up to July 2002 are grouped into Period III for convenience. Nine additional cases of geophagy were observed by field assistants ad libitum in this period (between December 2000 and July 2002), and are included in some general analyses presented below. The forest is demarcated into compartments according to logging activities and the study area is demarcated into blocks by a system of N–S and E–W observation trails that intersect each other at 100 m intervals. The locations of observation and collection sites were noted on this grid system.

Samples of ingested and control soil samples were collected at the time geophagy was observed. All samples were collected in plastic bags and taken to the camp laboratory, where they were air dried at room temperature and subsequently mailed to Mahaney, York University, for analysis.

Laboratory Protocols

Part of the protocol for behavioral observations in Period I included the collection of fecal samples from focal individuals during observations and ad libitum from other community members when possible. One gram of feces was weighed, and stored in 5.0-ml Corning plastic tubes and fixed with 10% neutral formalin. SG performed the parasitological analysis at the Primate Research Institute using the McMasters flotation and formol–ether concentration techniques. Eggs/gram (EPG) fresh dung was calculated for each sample as the mean value derived from three trials and is used here only as a relative measure of infection level.

Soil samples were analyzed at York University for particle size following procedures established by Day (1965). Electrode and electrical conductivity following Bower and Wilcox (1965) determined the pH. Carbon and nitrogen were analyzed on a Leco apparatus. Elemental analysis was undertaken at the SLOWPOKE-2 reactor at the Royal Military College of Canada using a modified version of the instrumental neutron activation analysis (INAA) procedures outlined by Hancock (1984). In this preliminary investigation, the concentrations of both short-lived and long-lived isotope-producing elements were determined.

Data Analysis

We analyzed the data using Fisher's Exact Test and Kruskal–Wallis ANOVA by rank. Significance was set at $P < 0.05$, and all analyses were two-tailed. Data elaboration was carried out using the package Statistica (Statsoft Inc., 1998) and InStat GraphPad (Ver. 2.01).

RESULTS

Behavior

General Description

In total, 23 cases of geophagy by 17 individuals (6 females, 11 males) were observed at Budongo, of which detailed information was obtained for four cases analyzed in greater detail in this paper. In all instances, chimpanzees removed soil from termite mounds. Chimpanzees broke open the termite mound of *Cubitermes speciosus* from any height of the mound. Both active and inactive mounds were targeted for geophagy. In 60% of these cases, termites were ingested along with the soil by breaking a clump of soil with termites inside. In such cases it was difficult to determine whether chimpanzees were mainly after the soil, the termites, or both.

We observed 6 of the 15 cases of geophagy during Periods I and II by five individuals on four different days. We observed one case of active sharing by a focal adult female with her infant male. On two more occasions, another individual approached and fed, or attempted to feed, from the same mound after seeing the first individual feeding from it. Time taken to ingest the soil ranged from less than 1 min to 12 min in duration, depending on the number of pieces consumed (range 1–4 pieces). Further behavioral details of the four cases of geophagy observed under focal-animal sampling are shown in Table 1.

Relative Frequency and Temporal Distribution

On the basis of focal observations, we calculated the relative frequency of occurrence of geophagy per 100 h for research periods I and II (Table 2). We noted a higher frequency of occurrence in Period I than in II. The combined mean relative frequency of occurrence was 0.79 instances of feeding on soil per 100 h of observation.

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All but one of the 23 cases of geophagy were observed before 1300 h, with a peak time of occurrence between 0900 and 1000 h. Interannual difference in the daily time of occurrence was negligible.

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Table 1. Details of termite mound soil ingestion observed in Sonso group chimpanzees during study Periods I and II

No.	Individual, date	Description
1	Kewaya (KY, adult female), August 22, 1998	This adult female, approximately 4 months pregnant, feeds on soil from a termite mound in block 7E at 1125 h. She exhibited no signs of illness. The whole process of eating soil took less than a minute. The soil that was eaten was not mixed with leaves or any other vegetation. KY feeds on the soil of the upper part. (soil sample Bud 2)
2	Kewaya (KY, adult female), August 25, 1998	At 0911 h, KY removes a piece of soil and feeds on it while en route to another tree. The soil consumed was found in block 5B and had previously been knocked down. One soil sample (Bud 3) was collected from a portion discarded by the chimpanzee and a second sample (Bud 3a) from an intact, active mound nearby.
3	Kwera (KW, adult female) and Kwezi (KZ, infant male of KW), August 27, 1998	At approximately 0854 h, KW climbs down from a tree, leaving KZ above, and breaks off a piece of soil with her hand from a termite mound, located in block 5B. KW rejoins her infant KZ up in the tree and begins to consume the soil. KZ stares intently at his mother. KW breaks off a piece of soil and hands it to KZ. KW holds one piece with her hand and one with her foot. Once that mouthful of soil is consumed, the infant puts his hand on his mother's mouth. KW then pushes the soil forward between her lips and KZ removes it and puts it in his mouth. KW continues to feed on the soil while KZ moves away. KW consumes the piece in her hand and then begins feeding on the one held in her foot. KZ reapproaches and reaches for a third piece of soil. KW bites off a piece and hands it to him. At this point the mother drops the remaining soil and climbs down at 0905 h. The discarded soil is collected for analysis as sample Bud 4.
4	Tinka (TK, adult male) and Gashom (GM, subadult), April 28, 2001	Two males, TK and GM, were observed to ingest soil at around 1200 h. The termite mound was about 0.5 m tall and built between the buttresses of a large *Cynometra alexandri* "ironwood" tree about 15 m from the north line transect of block GD. There was no vegetation growing in the mound, indicating it had been occupied by termites until fairly recently. The soil consumed was a lighter brown color than the surrounding soil. They each removed a sizable piece of soil, using only their teeth. Chewing on the soil took about 2 min before swallowing. TK ate four pieces and GM ate three. The soil was eaten in a normal way, neither reluctantly nor with speed. (soil sample Bud 1)

Table 2. Relative frequency of geophagy observed across chimpanzee study sites in East Africa

Site	Frequency, per 100 h	Reference
Uganda		
Budongo, Period I	1.42	This study
Budongo, Period II	0.17	This study
Kibale	0.52	Mahaney *et al.*, 1997
Tanzania		
Mahale	4.07	Mahaney *et al.*, 1996a,b
Gombe	8.33	Wrangham, 1977

Budongo: Period I (February 1998–October 1998): five cases in 352 h of focal observation; Period II (June 2000–August 2001): one case in 572 h of observation; Kibale (not specified): four cases in 767 h of focal observation; Kibale (January 1995–July 1996, 68% wet months): five times in 824 h; Mahale (November–December 1991, both wet months): five cases in 123 h of focal observation; Gombe: extrapolated from figure of 1/12 h year-round as estimated by Wrangham, 1977.

Monthly Distribution, Interannual and Regional Variation

Geophagy was observed in August 1998 (four observations; 8 months' study, February–September), December 2000 (one observation), March 2001 (two observations), and August 2001 (two observations) during a 16-month study period (June 2000–September 2001), and again in 2002: January (two observations), March, April, May, and July (one observation in each). There was no consistent trend in the occurrence of geophagy for any particular month of the year. The intermonthly pattern of occurrence and relative frequency of occurrence of geophagy was not consistent. Furthermore, we found no significant difference in the number of months in which geophagy was observed between the three study periods (Fisher's Exact Test, two-tailed, Period I–II: 4/8–3/16 months, $P = 0.39$, NS; Period I–III (4/8–5/10, $P = 1.00$, NS; Period II–III (3/16–5/10, $P = 0.19$, NS). It appears to us that the stimuli inducing geophagy are dynamic, and suggests that geophagy at Budongo is not simply a habitual year-round behavior but a condition-specific reaction or craving brought on by changing external environmental factors that can affect the physiology of the chimpanzees.

Our data suggest that, compared to other East African study sites for which such data are available, the frequency of occurrence at Budongo is relatively low (Table 2). Kibale, another Ugandan site, also has a relatively low frequency of occurrence. Great variability exists between these Ugandan and Tanzanian sites. In Tanzania, Mahale and Gombe have much higher rates of occurrence. These two sites are highly seasonal in their annual rainfall patterns, with as much as half of the year classified as the dry season (<100 mm). Budongo and Kibale on the other hand have only 1–2 months a year with less than 50 mm of rainfall. Seasonality of rainfall affects food availability, which in turn is expected to affect dietary choice. If geophagy is influenced by diet, interregional differences in the seasonality of food availability may be responsible in part for this interregional variation in the relative frequency of occurrence of geophagy.

Diet and Health

Food Selection and Geophagy

Here we analyze changes in food item selection to test for possible group-level dietary shifts that may help explain the fluctuating pattern of geophagy observed in this study. We used focal observation data from Period I to analyze for possible differences in the amount of time spent feeding on food items before (July), during (August, the month we observed geophagy in this study period), and after (September). We found no significant differences in the amount of time spent feeding on three major food items: seeds (Kruskal–Wallis $H(2, n = 29) = 2.38$, $P = 0.31$), fruits (Kruskal–Wallis $H(2, n = 29) = 3.18$, $P = 0.20$) and leaves (Kruskal–Wallis $H(2, n = 29) = 1.08$, $P = 0.58$).

During Period II, we collected a total of 2107 scan samples involving feeding behavior. In total, 72% of the scans represented feeding on fruits, 15.1% on young leaves and 7.4% on flowers. Feeding on other items such as bark represented the remaining 5.5%, pith, seeds, wood, soil and insects. We conducted a preliminary analysis of the monthly dietary change over the course of Period II using this scan sample feeding data to evaluate the effects of changes in the amount of fruit, leaf, or flower consumption by month as possible stimuli for geophagy. The monthly average was 69.92% (SE = 17) for fruits, showing the strong preference for fruits and their high availability year round. The monthly average was 14.08% (SE = 9) for leaves and 8.0% (SE = 11) for flowers.

As noted above, we observed geophagy in the months of December, March, and August. Months in Period II were classified as being high or low months of consumption of each of the three food items, based on whether they fell beneath or above the mean monthly average rate of consumption for each item. On the basis of this ranking, no significant relationship was found for the occurrence of geophagy and the relative amount of time spent feeding on any of these items (fruit, flowers: $P = 1.00$; leaves: $P = 0.52$; Fisher's Exact Test, two-tailed test).

The above results from Periods I and II must be interpreted with caution, however, because the level of analysis is at group level. The limited amount of data for the individuals observed eating soil preclude us from conducting any further detailed analyses during either period. Finer-grained analysis at the individual level is needed to properly address this question any further.

Health Status and Geophagy

We conducted a preliminary evaluation of parasite infection in individuals observed during Period I to evaluate the effects of intestinal parasite infection as a possible stimulus for geophagy (Table 3). In Period I all cases occurred in August, a wet month (rainfall >100 mm). According to these parasite profiles, we verified all individuals to be infected by at least two nematodes (*Oesophagostomum* sp. and *Strongyloides fulleborni*) and a protozoan *Troglodytella abrassarti*. Fecal samples were not available for the two adult males, TK and

Table 3. Parasitological profiles of individuals observed eating soils and control individuals sampled around the same period

		Identified parasite species		
Subject	Date[a]	*Troglodytella abrassarti*	*Oesophagostomum* sp.	*Strongyloides fuelleborni*
Observed eating soil				
KW	19	+ + +		
	25	+ + +	+ (3)	
	27	+ + +	+ (4)	
KY	19	+	+ (1)	+ (3)
	22	+ + +		
	22	−		
Controls				
ZA	29	+++	+ + (39)	
MG	27	+++	+ (2)	
TK	19	+++	+ (5)	+ (5)
VN	17	+	+ (5)	
ZT	13	+++	+ (2)	

Profiles based on modified MGL methodology: + = 1–9 eggs per preparation; ++ = 10–99 eggs/protozoa per preparation; + + + = 100 + eggs/protozoa per preparation; (EPG count) per preparation (18 × 18 mm); − = Negative.
[a] All dates from August 1998.

GM, but they did not appear to be overtly ill. No sign of physical illness, such as coughing or diarrhea, were noted in any of the individuals observed, although one female (Kewaya) was pregnant at the time. Compared to parasite levels in individuals observed during the same period, but for which geophagy was not observed, no marked difference in infection levels or species number were noted.

Physicochemistry

Characteristics of Ingested and Control Soil Samples

In Period I, four soil samples (Bud 2, 3, 3a, and 4) from termite mounds ingested by chimpanzees were collected (Table 4). In Period II, one sample (Bud 1) and a control (Bud 5) were collected. The control sample was collected 10 m from the termite mound to avoid any contamination from the mound itself. Soils surrounding the termite mound were observed to be quite uniform and the materials collected representative of uneaten soils. The control sample was collected at a depth of 15 cm, just sufficient to avoid the topsoil organic matter covering the forest floor. Samples were collected from a piece of soil discarded by the chimpanzee or from the same mound. In one instance (Bud 3a), the chimpanzee had chosen soil from a previously knocked down, inactive mound. Soil from a nearby active mound was also sampled, so the species of termite could be determined.

Table 4. Particle-size distributions in the Budongo termite mound soil and a ground soil control sample

Sample	% Sand (2000–63 μm)	% Silt (63–2 μm)	% Clay (<2 μm)
Ingested			
Bud 1	47.8	40.1	12.0
Bud 2	41.7	23.3	35.0
Bud 3	25.3	18.7	56.0
Bud 3a[a]			
Bud 4	27.9	34.9	37.2
Mean	35.9	29.3	35.1
SD	10.8	9.9	18.0
67% Range[b]	24.9–46.5	19.3–39.2	17.0–53.1
Control			
Bud 5	50.5	35.7	13.8

[a] Insufficient sample material available for analysis.
[b] ±1 standard deviation.

Soil Structure

Observations on aggregates of soil preserved in the laboratory sample show three or four distinct subsets (Table 4). A dark brown color is prominent on the concave sides of cavities that appear to be feces of round flat forms, not unlike cow dung in form. Similar dark-colored material is present on the convex sides of the above shells that appear to be openwork adobe material, including some quartz and magnetite grains up to 2 mm in size. The binder appears to be the darker silty clay variety of soil. Within the shells is a light-brown clayey silt. The shells appear to be remnant structures from the termite nest. Tube-shaped openings provide access to the chamber that is of the order of centimeters in size. In some samples, large quartz grains as well as some structures of darker soil stand above the level of the concave surface. Occasionally, a layering in the finer-grained concave walls is apparent, and in some cases a concentric structure reminiscent of drop-forms is apparent. Occasionally termite body parts appear in the matrix of the soil, including both mandibles and head of *Cubitermes.*

Particle Size

The particle size distributions shown in Table 4 indicate vastly different proportions of sand (25–48%) and clay (12–56%) among the ingested samples. Buds 2–4 range in texture from clay loam to clay. The Bud 3 sample is essentially a claystone. The control samples contain more sand and less clay, and may be classified as sandy loam, with little clay-size material. Although the limited number of samples available precludes formal statistical testing, the textural differences between ingested and uneaten materials are considered significant. For example, according to the sample standard deviation (ingested samples), there is a less than 16.5% chance that clay content would be less than 17.0% or sand content greater than 46.5% (Table 4). Silt content varies among samples, but differences between the ingested and control soils do not appear to be significant.

Mineralogy of the Sand and Silt Fraction

The sand and silt includes a mixture of strongly cemented soil and angular quartz in the coarse fraction. Medium sands are composed of angular quartz, representing basement gneiss mineralogy. Fine sands and silts include an assortment of round worn mineral grains, including rutile, zircon monazite, and Ti–Fe oxides. These minerals come from tillite beds (ancient glacial materials) near the head of the watershed south of the limit of the forest. At the site, this fine-grained worn material represents alluvium deposited within locally derived residual grit.

Mineralogy of the Clay Fraction

The <2-μm fraction of the samples analyzed in the ingested group has a clay mineral component that is exclusively kaolinite, halloysite, and metahalloysite. These clay minerals all belong to the 1:1 (Si:Al = 1:1) group and in the present case exhibit excellent crystallinity. Kaolinite is the most abundant, followed by metahalloysite and halloysite. The primary mineralogy of the ingested samples includes small amounts of quartz, mica, and plagioclase feldspar. While these minerals could supply small quantities of Si, Al, O, and a range of metal cations, there is no known nutritional/dietary/pharmaceutical significance to their presence in the sample suite. Within the control group (Bud5), only one sample had sufficient mass to warrant clay and primary mineral analysis. The trace from Bud 5 showed moderate amounts of metahalloysite but no kaolinite or halloysite, along with limited quartz and virtually no feldspar or mica within the primary minerals.

Au: The sentence discussing a clay mineral printout purportedly in Figure 8.7 has been deleted, since no artwork has been provide with this chapter. Please check.

Yes, deletion is fine.

Soil Chemistry

Colors of the dried samples shown in Table 5 range from a reddish brown hue (5 YR) for the ingested samples to a lighter 10YR color for the control (Bud 5). The colors indicate advanced liberation of Fe and, in some cases, incorporation of organic matter in small quantities. Indeed, the Bud 1 clay slurry in the laboratory showed the presence of white-colored microbes, presumably bacteria, after dispersion and particle size analysis. The pH of the ingested samples ranges from alkaline (Bud 4) to slightly (Bud 1 and 3) and moderately (Bud 2) acidic. The control sample is slightly acidic, with a pH of 6.1 recorded.

The total salt content as indicated by electrical conductivity (Table 5) is low in Bud 1, 3, and 4 and somewhat higher in Bud 2. In general the conductivity is close to the control sample, as expected in well-drained and leached tropical soils.

Table 5. Selected physical and chemical characteristics of soils in the Budongo sequence

Sample	Dry color	pH (1:5)	Electrical conductivity (μS/cm)	C (%)	*n* (%)
Ingested					
Bud 1	7.5YR 5/6	6.20	164	3.7	0.40
Bud 2	7.5YR 4/3	5.55	734	[a]	[a]
Bud 3	7.5YR 3/4	6.12	367	[a]	[a]
Bud 3a	10.0YR 5/1	[a]	[a]	[a]	[a]
Bud 4	10.0YR 5/3	7.58	420	[a]	[a]
Control					
Bud 5	10YR 5/4	6.12	153	2.9	0.27

[a] Insufficient sample material available for analysis.

The elemental chemistry of ingested and uneaten soils is shown in Table 6. Consistent with the clay mineralogy, the most abundant measured element is Al, comprising 5.8–7.5% by weight of each sample. Iron is also abundant (1.7–5.7%), particularly in the ingested soils. While Mg comprises about 1.0–1.25% by weight of the soils examined, other major elements (Ca, K, Na, and Ti) are relatively rare. Trace elements detected using the INAA procedures include As, Br, and Cr. Iodine was usually below detection limits.

Here too, statistical testing is limited by the small sample sizes available; however, once again considering the standard deviation of the ingested materials,

Table 6. Concentration of chemical elements in the Budongo sequence

Sample	Al (%)	Ca (%)	I (ppm)	Mg (%)	Mn (ppm)	Na (%)	Ti (ppm)	K (%)	As (ppm)	Br (ppm)	Fe (%)	Cr (ppm)
Ingested												
Bud 1	7.54	<0.20	<7.7	–	1376	0.06	8998	0.27	3.24	15.0	5.70	102.0
Bud 2	6.37	0.34	<6.3	1.24	1281	0.07	8560	0.32	1.71	14.1	4.20	86.0
Bud 3	6.91	0.30	<4.6	1.23	878	0.04	6716	0.19	2.43	11.4	4.64	91.1
Bud 3a	6.01	0.39	<6.9	–	1181	0.05	6980	0.17	2.67	17.9	4.39	79.0
Bud 4	6.87	0.38	9.1	1.06	798	0.04	7014	0.21	2.85	11.6	4.65	89.7
Mean	6.74	0.33	–	1.18	1103	0.05	7654	0.23	2.58	14.0	4.72	89.6
SD	0.58	0.05	–	0.10	253	0.01	1054	0.06	0.57	2.68	0.58	8.39
Plus[a]	5.58	0.23	–	0.98	597	0.04	5564	0.11	1.44	8.70	3.56	77.8
Minus[b]	7.90	0.42	–	1.38	1609	0.07	9744	0.35	3.72	19.4	5.88	106.3
Control												
Bud 5	5.81	0.36	<5.6	1.00	1098	0.05	7550	0.89	1.00	8.17	1.67	52.9

[a]±2 standard deviations.

significant differences between ingested and uneaten materials appear to occur with at least 5 of the 11 elements measured. Table 6 gives the two standard deviation ranges (95% confidence interval) for ingested sample materials assuming elemental concentrations are normally distributed. In the control sample As, Br, Cr, and Fe fall below this range while K falls well above. Al and Mg also appear to be less abundant in the uneaten control soil. The most significant differences between the two soils occur in the case of Fe and K. While the former is on average 2.8 times more abundant in the ingested materials, the latter appears to be depleted by approximately 75%. Given the range of variability in Ca, Mn, Na, and Ti among samples, there is no evidence of any differences between the ingested and uneaten materials on the basis of the concentration of these elements.

DISCUSSION

This is the first detailed report of geophagy in chimpanzees of the Budongo forest. While it is clear that chimpanzees are selecting termite mound clay, they also appear to be selecting termites themselves in many cases. The size of our data set is admittedly small, which prevents an in-depth analysis of the possible ecological or health-related factors responsible for geophagy in this population. Nonetheless, we were able to add new insights into geophagy in primates in general, provide new details from this site, and further confirm trends in the chemical and mineralogical contributions of the soils selected by chimpanzees for consumption across East Africa.

Anecdotal evidence suggests that on some occasions around the time geophagy was observed, individuals in the group were suffering from gastrointestinal upset (i.e., diarrhea), suffering from influenza-like symptom (i.e., coughing), or were feeding excessively on unripe fruits. Some of these symptoms might have been partially relieved by the ingestion of clay. From our analyses to date, we have established that, like other previous reports of geophagy in primates, a major self-medicative value of this behavior is likely to be its ability to soothe the stomach via the physical absorption of stomach acids and plant or pathogen-related toxins in the gut. Future studies of geophagy will require greater real-time correlation at the individual level between diet and geophagy to more adequately address the immediate stimuli for and effects of geophagy.

The geomorphic "flat" on which the termite mound occurs most likely is an alluvial landform—either a floodplain or terrace. The abundance of monazite in the heavy mineral fraction of the Bud 1 soil implies probability of a Ce anomaly in the light rare-earth elements. Chromium, which may be an important microelement in nutrition, identified by INAA is derived from Cr–Fe oxide in the heavy mineral suite. The geological source is not apparent in basement gneiss. It may be derived from the tillite in the headwaters of the drainage or from unmapped units in the basement complex.

The ingested soil is high in percent clay relative to controls. The clay mineral composition of the ingested material includes kaolinite, halloysite, and metahalloysite in varying proportions but with kaolinite making up more than 50% of the material in every case. The abundance of kaolinite specifically distinguishes ingested materials from uneaten controls and this appears to be a common phenomenon at sites throughout Africa where chimpanzees are attracted to ancient land surfaces in their quest for earth materials for ingestion (Mahaney *et al.*, 1998; Mahaney, 1999; Mahaney & Krishnamani, 2003). It may be no coincidence that older soils also contain better-developed clay mineral crystals, since refined (pharmaceutical-grade) crystallinity is characteristic of over-the-counter remedies for gastrointestinal upset, such as Pepto-Bismol™ and Kaopectate™. Chimpanzees may consume clay, and especially kaolinite-based soils, to offset gastric upsets and diarrhea and not to negate the positive effects of this for seed dispersal (e.g., Plumptre *et al.*, 1994).

Differences in the chemistry of the ingested and uneaten soils largely correspond to changes in clay content, and support its possible role in stimulating geophagic behavior. Modest increases in Al as well as trace elements, which may occur as adsorbed cations (As, Br, and Cr), are consistent with the observed increase in overall clay content. The differences in Fe and K, however, reflect changes in clay mineralogy, and specifically a shift to more advanced weathering products such as kaolinite or iron oxides (which may occur in trace amounts). While clay content may provide an ultimate (i.e., medicinal) explanation for soil ingestion, it should be noted that differences in color (e.g., reddish hues due to Fe) and potentially odor or taste, as well as site context (i.e., termite mound centennials), may assist chimpanzees in identifying suitable soils for ingestion.

It is noteworthy that subjects were observed attempting to exploit more indurate soils at the base of the termite mounds as well as at the top, since color, odor, and taste rather than texture would distinguish this material from the uneaten control soils. The olfactory response to this material may be the clayey soil, characterized as having an unctuous odor. Similarly, maillot has a distinctive smell and is prominent in the soil in association with the remains of termites within the cell walls of in situ soil crumbs as well as on grains retrieved in sieve analysis. The fungus *Penicillium* is prominent on mounds of *Odontotermes* and *Pseudacanthotermes* (Ketch, 1998; Ketch *et al.*, 2001).

Au: Note the change of Ketch, 2001, to Ketch et al., 2001.

OK, Thanks!

It is uncertain from the limited number of elements analyzed whether the ingested soils might help counter nutritional or other dietary deficiencies. While the carbon and nitrogen analyses are a minimum, the trend reported here indicates that the ingested material is higher in carbon (possibly because *Cubitermes* is humiverous, and both building material food and feces tend to be richer in carbon), which means the bacteria, mold, and fungi counts are higher as well, a factor we have not seen at other geophagy sites. This may mean the organisms have found a microbe that is beneficial to them, possibly one that fights off disease, and chimpanzees may benefit from this too. Further research is required to determine if there is a microbial substance in the ingested material that is of pharmaceutical importance to the chimpanzees (e.g., Ketch, 1998; Ketch *et al.*, 2001). Consideration should be given as to the effect of the tree species (*Celtis durandii* syn. *C. gomphophylla* Bak.) found in association with this eaten *Cubitermes* mound soil as it differs from species documented elsewhere (e.g., *Cynometra alexandri* Wright (Ironwood); Newton-Fisher, 1999b). The contiguous root system around the respective mounds may also impart a biogeochemical character to the soil that prompts its consumption.

Future work at Budongo on aspects of self-medication and disease are strongly encouraged, and are expected to provide a body of information invaluable for comparison with other long-term great ape study sites across Africa where similar data is now being collected. Beyond the direct value of such studies in better understanding the ecological and disease-related impacts on behavior, these studies are expected to add essential information for the conservation of great apes and their habitats across Africa.

Tweheyo Mnason's...

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