CHAPTER EIGHT

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

A Multidisciplinary Study

Mnason Tweheyo, Vernon Reynolds, Michael A. Huffman, Paula Pebsworth, Shunji Goto, William C. Mahaney, Michael W. Milner, Anthony Waddell, Randy Dirszowsky, and Ronald G. V. Hancock

---

Mnason Tweheyo • Department of Forest Biology and Ecosystems Management, Makerere University, Kampala, Uganda **Vernon Reynolds** • School of Anthropology, University of Oxford, 51 Banbury Road, Oxford OX2 6PE, United Kingdom **Michael A. Huffman, Paula Pebsworth, and Shunji Goto** • Primate Research Institute, Kyoto University, Kanrin 41-2, Inuyama, Aichi 484-8506, Japan **William C. Mahaney, Michael W. Milner, and Anthony Waddell** • Geomorphology and Pedology Laboratory, York University, 4700 Keele St., North York, Ontario, Canada M3J 1P3 **Randy Dirszowsky** • Geomorphology and Pedology Laboratory, York University, 4700 Keele St., North York, Ontario, Canada M3J 1P3, and Department of Chemistry and Chemical Engineering, University of Toronto, Toronto, Ontario, Canada K7K 7B4 **Ronald G. V. Hancock** • Department of Chemical Engineering and Applied Chemistry, University of Toronto, Toronto, Canada M5S 1A4.

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

INTRODUCTION

Geophagy occurs widely among primate species (Krishnamani & Mahaney, 2000). While reported for chimpanzees in the wild since the 1960s (Hladik, 1977; 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.*, 1996b; 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.

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, 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, 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, 1999b; Tweheyo, 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.

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.

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.

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^{TM} and Kaopectate^{TM}. 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).

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.

ACKNOWLEDGMENTS

NORAD funded Mnason Tweheyo's PhD research work in Budongo. Michael A. Huffman's work in Budongo was funded by a grant from the Leakey Foundation, and the J. William Fulbright Scholarship Foundation funded Paula A. Pebsworth. The physicochemical and mineralogical analyses were funded by Quaternary Surveys, Toronto. NORAD, National Geographic Society, the Uganda National Council for Science and Technology, and the Uganda Forest Department provided invaluable support for all research at Budongo. We are grateful to Professor Kaare Lye of the Agricultural University of Norway, Dr. John Kaboggoza of Makerere University, and Monday Gideon Mbotella and Kiwede T. Zephyr for their direct input and assistance. We extend our thanks and appreciation to all the research assistants and support staff of the Budongo Forest Project. Dr. Tim Myles, University of Toronto, provided assistance in the identification of *Cubitermes* remains in the soil samples. Last but not least, we thank Massimo Bardi for his valuable advice in the preparation of the paper and advice on data analysis.