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RESEARCH ARTICLE

Geophagy in Chacma Baboons: Patterns of Soil Consumption by Age Class, Sex, and Reproductive State

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Despite baboons' widespread distribution across Africa, geophagy among all subspecies has been poorly documented. We used video camera traps and soil analyses to investigate geophagy in chacma baboons (*Papio cynocephalus ursinus*) inhabiting the Western Cape of South Africa. During an 18-month study, from August 2009 to January 2011, we continually monitored the largest and most frequently visited geophagy sites with camera traps for 545 days and captured soil consumption at one or more sites on 266 of those days (49%). In 3,500 baboon visits to geophagy sites, video camera traps captured 58.6 hr of geophagy. From these data, we evaluated site preference based on time spent consuming soil among these four geophagy sites. One hundred and seventy days of soil consumption data from the most frequently visited geophagy site allowed us to look for demographic trends in geophagy. Selected consumed soils from geophagy sites were analyzed for mineral, physical, and chemical properties. The baboons spent more time consuming white alkaline soils with high percentages of clay and fine silt, which contained higher concentrations of sodium than non-white acidic soils that contained higher concentrations of iron. Our data indicate that pregnant chacma baboons spent more time consuming soil at monitored geophagy sites than baboons of any other age class, sex, or reproductive state. Based on analytical results, the soils consumed would be effective at alleviating gastrointestinal distress and possibly supplementing minerals for all age/sex classes, but potentially for different age/sex requirements. Am. J. Primatol. 73:1–10, 2011.

Key words: geophagy; gastrointestinal distress; sodium; camera traps; pregnancy

INTRODUCTION

Geophagy, the regular and deliberate consumption of natural earth materials, is widespread in the animal kingdom [Abrahams, 2005; Kreulen, 1985; Young et al., 2011] and has been reported in many primate species [Ferrari et al., 2008; Krishnamani & Mahaney, 2000]. Several nonexclusive hypotheses exist to explain the function and prevalence of geophagy among human and non-human primates (NHP): alleviation of gastrointestinal (GI) distress and upsets, supplementation of minerals and/or elements, antibacterial properties, and alleviation of hunger [Krishnamani & Mahaney, 2000; Setz et al., 1999; Young et al., 2011]. Because of these putative benefits to health, geophagy is considered a widespread form of self-medication among primates and other animals [Huffman, 1997, 2011].

Geophagic soils' ability to alleviate GI distress consists primarily of four additional nonexclusive hypotheses: (1) adsorption of toxins and plant secondary metabolites (PSM) [Dominy et al., 2004; Gilardi et al., 1999; Hladik, 1977a,b; Johns & Duquette, 1991; Klaus et al., 1998]; (2) antacid action [Davies & Baillie, 1988; Limpitlaw, 2010; Oates, 1978]; (3) antidiarrheal action [Mahaney et al., 1995a; Vondruskova et al., 2010; Voros et al., 2001]; and (4) relief from effects of parasitosis [Bicca-Marques & Calegaro-Marques, 1994; Knezevich, 1998]. In a review of all published primate geophagy studies, Young et al. [2011] found that 65% of reports attributed soil consumption as either probably or definitely motivated by clay's ability to detoxify PSM, protection from parasites and pathogens, and alleviation of some form of GI distress. An important component of geophagic soil is clay. It has been experimentally demonstrated that clay alleviates GI distress because it has the ability to

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bind with mucin and stimulate mucin production, which subsequently strengthens the epithelial cells that line the intestinal wall [Gonzalez et al., 2004]. Clay adheres to toxins, PSM, and organic molecules and reduces the permeability of the intestinal wall to bacteria, viruses, and toxins known to cause GI distress [Gilardi et al., 1999; Gonzalez et al., 2004; Johns, 1986]. Geophagic soils may also contain gibbsite, alkaline soluble salts, and carbonate minerals, which act as effective antacids [Abrahams, 1999; Wilson, 2003].

The supplementation of minerals and/or elements hypothesis suggests soil can provide minerals to the consumer that may be deficient in the diet [Ganzhorn, 1987; Heymann & Hartmann, 1991; Hunter, 1973; Kreulen, 1985; Mahaney et al., 2005; Wiley & Katz, 1998], and was cited as the stimulus for geophagy in 65% of primate studies according to Krishnamani and Mahaney [2000] and Young et al. [2011]. Sodium is the most common mineral cited as a stimulus for geophagy among all herbivorous animals [Holdø et al., 2002; Weeks & Kirkpatrick, 1976], but has never been cited as the stimulus for human geophagy [Young et al., 2011] and only rarely for NHP [Ganzhorn, 1987; Mahaney et al., 1993; Matsubayashi et al., 2007].

To demonstrate that minerals present in clay were available to human consumers, studies have investigated the mineral bioavailability of geophagic soils [Young et al., 2011]. The results of these studies suggest most geophagic studies have vastly overestimated the amount of minerals available from soil ingestion [Young et al., 2011]. Unfortunately, no NHP studies have demonstrated that minerals were bioavailable from soils consumed by primates. To further complicate the question of bioavailability, an in vitro experimental study demonstrated that geophagy might actually cause iron, copper, and zinc deficiencies owing to the clay's ability to bind micronutrients and prevent their absorption [Hooda et al., 2004].

The antibacterial hypothesis suggests that soil may possess antibacterial properties that provide protection from pathogens [Ketch et al., 2001; Williams et al., 2009; Williams & Haydel, 2010]. In vitro microbiological studies have demonstrated that clay is effective against numerous human bacterial infections [Williams & Haydel, 2010].

The famine food hypothesis suggests that soil functions as food during times of food scarcity [Abrahams, 2005; Aufreiter et al., 1997]. During actual famine, soil's function to assuage human hunger was documented in China, Germany, Lapland, Serbia, Finland, Italy, and Haiti [Young, 2011]. No studies have demonstrated that NHP use soil as food; it is doubtful, because soil is typically eaten in only small amounts at a time.

It has been suggested that the benefits of geophagy can be multifunctional and these functions can change over time [Davies & Baillie, 1988]. In the case of human geophagy, clay is uniquely associated with pregnancy in many traditional human societies [Hunter, 1993; Vermeer, 1966] and it has been suggested that it may serve several roles: relief from the symptoms of pregnancy sickness, adsorption of dietary toxins [Vermeer & Ferrell, 1985], and supplementation of minerals [Hunter, 1973; Wiley & Katz, 1998]. Despite the widespread prevalence of morning sickness in humans, it has not been confirmed in NHP. An association between geophagy, pregnancy, and lactation has been found in bats [Voigt et al., 2008] and elephants [Holdø et al., 2002], but to the best of our knowledge, no study has shown an association between geophagy and pregnancy in NHP species.

Primate geophagy studies have focused on chemical, physical, and mineral composition to explain why soil was consumed and what functional role it served [Bolton et al., 1998; Krishnamani & Mahaney, 2000; Setz et al., 1999; Wakibara et al., 2001], but consumption has not been investigated by age class, sex, or reproductive state. To provide more than just a description of soils, geophagic studies have begun to use camera traps to gain insight into this phenomenon that is not rare in animals, but remains poorly understood [Blake et al., 2010; Matsubayashi et al., 2007; Tobler et al., 2009].

To date, three studies have published cursory data relating to geophagy in baboons [Hall, 1962; Henshaw & Ayeni, 1971; Moolman & Breytenbach, 1976].

Our objective is to provide the first detailed report of geophagy for the genus *Papio* and specifically chacma baboons. This report describes soil consumption by age class, sex, and reproductive state, with an emphasis on geophagy with respect to reproductive state, as it is an area underrepresented in geophagy literature to date. Our results of soil analyses and camera trap images are discussed in order to test current hypotheses for the function(s) of geophagy. We hypothesize this troop of baboons used soil to alleviate GI distress and possibly to supplement minerals.

METHODS

Study Site

We conducted a field study at Wildcliff Nature Reserve located in the Western Cape, South Africa. The reserve (33°57′S, 21°2′E) is approximately 1,000 ha in area with elevations from 290 to 1,130 m. The southern boundaries of the reserve lie between the Hottentotsbosch and Plattekloof Rivers (Fig. 1). Wildcliff is composed of a variety of habitats, including mountain fynbos, renosterveld, afro-montane forest, meadows, and stands of alien *Acacia mearnsii*, *Pinus pinaster*, and *Quercus rogor*. The annual rainfall is approximately 400–600 mm, and

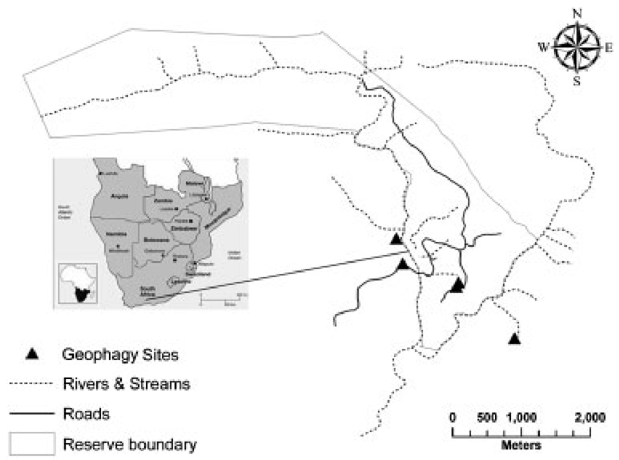

Fig. 1. Map of Wildcliff Nature Reserve, its location within South Africa, and five geophagy sites located on and around the reserve.

the mean annual temperature for 2009 and 2010 was 20.5°C.

We located five major geophagy sites on the reserve and in the surrounding area. Three of the five geophagy sites were created following anthropogenic disturbance: a road cut and an excavation site. The two remaining sites were naturally exposed surfaces. It has been suggested that geophagy sites are selected by smell, taste [Mahaney et al., 1990], and ''mouth feel'' [Bolton et al., 1998].

Our research complied with the laws of South Africa pertaining to biological field research, was authorized by CapeNature, and adhered to the American Society of Primatologists principles for the ethical treatment of NHP.

Study Population

Chacma baboons are widely distributed throughout Southern Africa. They occur in multimale/multifemale groups and are nonseasonal breeders. The study troop was semi-habituated and consisted of approximately 115 members. At the end of 2010, there were 6 adult males, 6 subadult males, 36 adult females, 63 juveniles, and 7 infants. Baboons are omnivorous, and this troop was observed to eat a variety of seeds, grasses, corms, forbs, flowers, fruits, and animal matter. The population steadily increased during the study period.

Camera Traps

We used digital camera traps (Covert SG550, Lewisburg, KY) activated by infrared motion and heat detection to document soil consumption at known geophagy sites. We positioned cameras approximately 20 cm above ground at the edge of four major geophagy sites frequented by the baboons; a fifth site, south-east of the reserve, was visited infrequently and was not monitored. One camera per geophagy site was adequate to cover the entire area in which baboons mined soil, with the exception of site one. This site was larger than the others; therefore, two cameras were used to monitor nonoverlapping areas of the site where soil was being mined and a second area where it had previously been mined. Cameras operated continuously, except when a two-gigabyte Secure Digital (SD) memory card became full, batteries failed, or a camera malfunctioned. We programed the cameras to take 59 sec videos with a 1 sec interval between videos, and all cameras were synchronized by date and time. Variation in the length of video capture did occur, but the data presented reflect the actual time soil was consumed. Images were date and time stamped. We checked cameras several times per week to insure they were functional and to exchange batteries and SD cards. Cameras were set up for varying lengths of time based upon discovery and access.

Camera Trap Analyses

Each camera trap video was scored to document the date, arrival and departure time, age class, sex of each baboon, and reproductive state of adult female baboons. The identity of an individual was documented, if known. If age class or sex could not be identified, the individual was listed as ''unknown,'' and these data were included in total soil consumption but excluded from further analyses. Soil ingestion time was summed across successive videos and recorded from the time the baboon first began to eat soil (biting, chewing, swallowing), until the time they stopped eating soil. If the individual was absent from the successive video, the ending time of soil consumption was the time the individual was last seen feeding on soil. Typically, the baboons would stop feeding, turn, and leave the geophagy site. If they were to move from one section of the site to another, the time used to relocate was subtracted from the total time spent feeding on soil. If they stopped feeding on soil, and remained at the site to engage in a subsequent behavior (groom, copulate, play) the time spent feeding on soil stopped the second they turned away from the geophagy site. It was found that baboons visited the same geophagy site only once a day; therefore, these data were organized by day so the requirement of independence was met. These records of geophagy by individual, from a given day, were then combined with other records of the same age class, sex, and reproductive state. The time spent consuming soil for each category was totaled and averaged. It was these combined and averaged values that were statistically analyzed. Owing to steep terrain and proximity to water, cameras at sites two, three, and four were located further from the mined areas than site one, and did not yield the same quality of images. Fortunately, site one was frequented the most and yielded the best images so an additional criterion, intrasite consumption, was documented at this site. This area is approximately 400 cm in length, and four sections of approximately 100 cm long were established. The site has several ''landmarks,'' which made it possible to document where soil consumption occurred.

Baboons were separated into four categories: adult male, subadult male, adult female, and juvenile based on physical development and reproductive maturation [Altmann et al., 1981]. Sex determination of juveniles from camera trap videos was often difficult; therefore, this age category combines both males and females. Infants were excluded from the analyses because, although they did explore the geophagy site and occasionally consumed small amounts of soil, the mother's proximity to the infant often obscured visibility of their feeding behavior from the camera. Age group classification was based on criteria established by Altmann et al. [1981]. Adult females were classified as nonswelling, swelling, pregnant, or lactating based on sex skin turgescence, paracallosal skin coloration, and presence of infant [Altmann, 1970; Altmann et al., 1981; Bercovitch, 1999]. Baboons display an external marker of pregnancy: the paracallosal skin changes from black to scarlet the second week after the expected time of missed menstruation [Altmann, 1970; Gilbert & Gilman, 1951]. As the pregnancy progresses, the perianal and perivaginal areas turn intense scarlet [Gilbert & Gilman, 1951]. We were able to exploit this pregnancy sign and, in conjunction with camera trap images, investigated geophagic behavior by reproductive state (Fig. 2).

Occasionally, glare on cameras, condensation, or baboons positioned immediately in front of the cameras impacted video quality. Visits with poor visibility or forcible displacements were excluded from statistical analysis but were included in the raw database, which documented total time spent consuming soil at all geophagy sites.

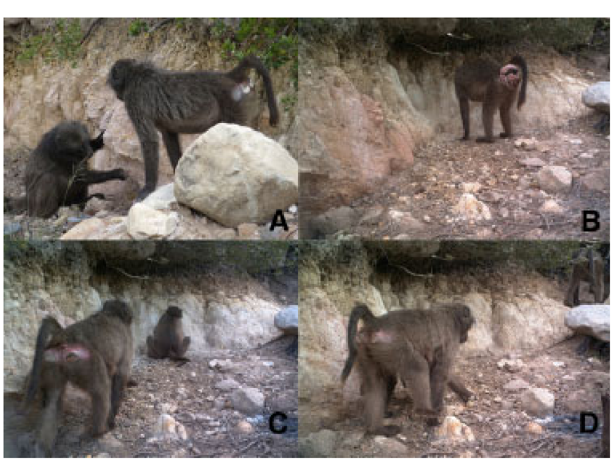

Fig. 2. Reproductive states; **A**, nonswelling; **B**, swelling; **C**, pregnant; **D**, lactating (infant is clinging to the female's ventrum).

Soil Analyses

To gain a better understanding of what possible benefits soil provided the Wildcliff baboons, we randomly collected 12 soil samples from four major geophagy sites where fresh teeth and nail marks were observed. Soils were analyzed by the Central Analytical Facility at the University of Stellenbosch for pH, particle size, X-ray diffraction (XRD), X-ray Fluorescence (XRF), Atomic Absorption Spectroscopy (AAS), and Ion Chromatograph (IC) to determine physical, chemical, and mineral composition. Analytical techniques requiring an extraction were performed using a ratio of 10 g of soil to 50 ml of water. The geochemical and mineralogical results presented here will focus on two soil characteristics, which have been previously cited as possible stimuli for geophagy: iron [Abrahams & Parsons, 1997; Hunter, 1973; Mahaney et al., 1997] and sodium [Ganzhorn, 1987; Mahaney et al., 1993; Matsubayashi et al., 2007].

Control samples were not taken. Previous studies have failed to show differences between consumed and unconsumed soils that were taken from adjacent areas of exposed geophagy sites [Inoue, 1987; Mahaney et al., 1995b; Müller et al., 1997]. We suggest there is questionable validity in taking soil ''control'' samples adjacent to areas where soils are consumed. The absence of teeth and nail marks cannot function as proof that these areas will not be mined in the future. However, if it can be established what areas or soil horizons are never consumed, analyses of these unconsumed soils and a description of the landscape can yield valuable information on the commonality among consumed soils [Mahaney & Krishnamani, 2003]. We never observed the baboons to consume surface soils. Therefore, we have provided a description of the landscape at geophagy site one, which was frequented the most and whose soil horizons are obvious from the soil profile, in an effort to illuminate the difference between these unconsumed and consumed soils.

Statistical Analysis

Nonparametric analyses were performed to analyze the dataset using SPSS 13.0 (SPSS, Inc., Chicago, IL), given that the assumption of normality was not met by the included variables. Friedman tests were used to determine the effect of age, sex, and reproductive state on the number and duration of visits, by categories, to the geophagy sites. At geophagy site one, we determined that individuals did not use this site twice in the same day. Therefore, organizing the data collected by day allowed us to maintain independence of each datapoint. Duration of visits was always measured in seconds, but using a different unit of measure, such as minutes, would not affect the statistical results. Post hoc Wilcoxon tests were used to detect significant differences between groups (i.e., females vs. males). A significance level of P less than or equal to 0.05 was selected for all tests. We used Spearman Rank Order Correlation to measure the strength and direction of associations among duration of soil consumption, rainfall, and temperature. Kruskal–Wallis tests were used to detect significant differences among geophagy sites for iron and sodium.

RESULTS

Soil Consumption

From August 2009 to January 2011, camera trap videos captured soil consumption on 266 out of 545 days (49%). In 3,500 recorded visits to the sites by individual baboons for soil consumption, the cameras documented 3,516.6 min or 58.6 hr of geophagy. Time spent consuming soil by all individuals ranged from 1 to 690 sec, with an average time of 62 sec. There was considerable intersite variation in relation to frequency and duration of soil consumption (Table I).

Site 1 was monitored the longest, was frequented the most, and provided the best video images. Nevertheless, of the 188 days that this site was frequented, 18 days of data were excluded from statistical analyses owing to poor video images or camera failure. Therefore, the remaining 170 days of data from this site were used for statistical analyses and to investigate differences among age class, sex, and reproductive state. The two cameras at site one documented different behavior. One camera captured soil consumption, whereas the other camera captured locomotion to and away from the geophagy site. This second area served as a small corridor not only for the baboons but also for mongoose, genets, and a resident leopard. Despite the fact that soil was not consumed in this area, we continued to monitor this corridor as it has been suggested that geophagy sites can potentially be an area where predators wait for prey [Matsubayashi et al., 2007]. We found no evidence of predation at this frequently used geophagy site during the study.

Seasonality of Geophagy

We found no relationship between rainfall (mm) and duration of time spent consuming soil between months for: all individuals ($r_s = -0.12$, $N = 17$, $P = 0.65$), adult males ($r_s = -0.13$, $N = 17$, $P = 0.63$), adult females ($r_s = -0.229$, $N = 17$, $P = 0.38$), and juveniles ($r_s = 0.01$, $N = 17$, $P = 0.98$). We also found no relationship between average daily temperature (°C) and duration of time spent consuming soil between months: all individuals ($r_s = -0.092$, $N = 17$, $P = 0.73$), all adult males ($r_s = 0.19$, $N = 17$, $P = 0.46$), all adult females ($r_s = 0.16$, $N = 17$, $P = 0.55$), and juveniles ($r_s = -0.10$, $N = 17$, $P = 0.72$).

Differences in Geophagy by Age Class and Sex

Analyses of age class and sex showed 205 (6%) visits to geophagy sites were by adult males, 274 (8%) were by subadult males, 975 (29%) were by adult females (all reproductive states), and 1,880 (56%) were by juveniles. In an additional 44 observations (1%), the age class or sex could not be determined. The high frequency of juvenile visits reflects the fact that more than half of the troop was composed of this age class. Therefore, subsequent analyses were weighted to reflect troop demographics and classes were analyzed using averages. We found no significant differences between adult and subadult males in both number of males and total time spent consuming soil at the site (number of males: $Z = -0.10$, $P = 0.91$, $N = 170$; total time spent consuming soil: $Z = -0.37$, $P = 0.70$, $N = 170$). Therefore, these values were combined and will be referred to as ‘‘adult’’ males.

Our data indicated a statistically significant difference in the time spent per category by adult males, all adult females, and juveniles per day consuming soil. On average, each individual female spent 92 sec/day feeding on soil, males spent 60 sec/day, and juveniles 48 sec/day (Friedman test: X^2 (2) = 50.60, $N = 170$, $P < 0.001$). There was, however,

TABLE I. Characteristics of Geophagy Site Use

Geophagy site	♯ camera days	♯ days baboons visited site	% days visited	Total ♯ of observations	Total duration of soil consumption (sec)
1[a]	545	188	34.5	2,061	150,737
2[b]	402	83	20.6	969	42,160
3[b]	402	45	11.2	226	5,738
4[c]	242	23	9.5	122	12,363

Soil consumption by all baboons from four different geophagy sites.
[a]Monitored from July 30, 2009 to January 26, 2011.
[b]Monitored from July 30, 2009 to September 5, 2010.
[c]Monitored from January 6, 2010 to September 5, 2010.

no significant difference between individual feeding times for adult males and juveniles (post hoc Wilcoxon test: $Z = -0.903$, $P = 0.37$, $N = 170$).

Additionally, we calculated differences in the average time spent consuming soil per individual per day among all reproductive states and found a statistically significant difference (Friedman test: X^2 (3) = 20.72, $N = 170$, $P < 0.001$) (Fig. 3). The time spent consuming soil by pregnant and nonswelling individuals was significantly different from lactating and swelling individuals. However, the difference between pregnant and nonswelling was not statistically significant (Wilcoxon signed rank test: $Z = -0.886$, $P = 0.38$, $N = 170$) nor was the difference between swelling and lactating females (Wilcoxon test: $Z = -0.4976$, $P = 0.62$, $N = 170$).

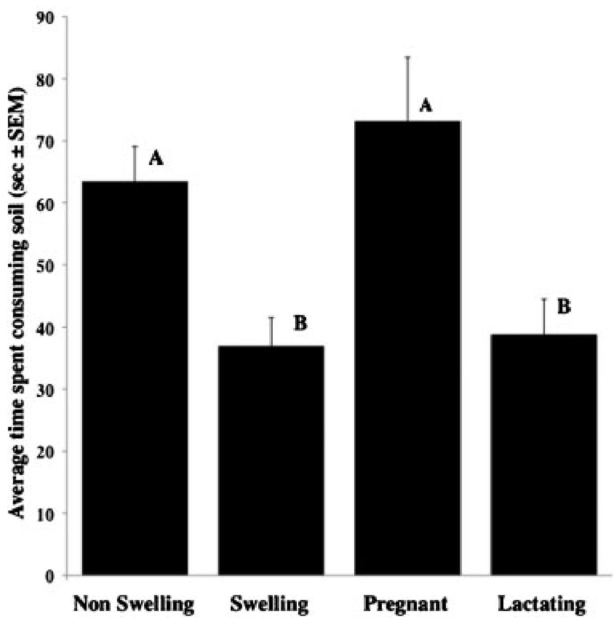

Fig. 3. Differences in average time spent consuming soil between reproductive states. Soil consumption for categories labeled "**A**" were significantly different from categories labeled "**B**."

Geology and Geochemistry

As previously mentioned, three of five geophagy sites were created following anthropogenic disturbance: a road cut and an excavation site. The two remaining sites were naturally exposed surfaces. Geophagy site one, which was created by a road cut, provides a unique opportunity to explore what soils or horizons were consumed and not consumed. The terrain surrounding this site is steep and hilly and the soils are primarily ochre in color. From the soil profile, there seems to be a discontinuity between the surface unconsumed soils and the consumed soils, as they appear to be a weathered bed remaining from an ancient horizon. The commonality among the four geophagy sites frequently visited by the Wildcliff troop was high percentages of clay and silt and low percentages of sand. Three of the four geophagy sites were characterized as very strongly alkaline, but the fourth site, which was frequented the least, was very strongly acidic (Table IIa). Iron (Fe_2O_3) was analyzed by XRF and there was significant variation (wt%) among the four geophagy sites (Kruskal–Wallis test: $X^2 = 6.78$, df = 2, $P < 0.05$). Sodium was measured on AAS and variation among the geophagy sites was not statistically significant (Kruskal–Wallis test: $X^2 = 3.88$, df = 2, $P = 0.144$). Geophagy site one was preferred by the baboons and contained higher percentages of clay and lower percentages of sand. Sections B and C within geophagy site one were

TABLE II. Geochemical Characteristics of Geophagy Sites (a) Physical, Chemical, and Mineralogical Properties of Soils From Four Geophagy Sites Used by Baboons. (b) Intrasite Variation Within Geophagy Site 1 for Particle Size (Sand, Silt Clay), Sodium, Iron, Time Spent Consuming Soil, and Color of Soil

Site ♯	pH	% sand	% silt	% clay	Na (ppm)	Fe_2O_3 (wt%)	Color
(a)							
1 ($n = 5$)	9.8	3.0	63.5	33.5	1,130.9	2.28	White and pink
2 ($n = 3$)	9.6	11.3	63.3	25.3	680.1	6.17	Ochre/pink
3 ($n = 3$)	4.6	7.1	65.9	27.0	519.3	5.28	Ochre/pink
4 ($n = 1$)	9.4	3.0	71.0	26.0	357.0	1.10	White

(b)

Section	Time (min)	% sand 2.0–0.05 mm	% silt 0.05–0.002 mm	% clay < 0.002 mm	Na (ppm)	Fe_2O_3 (wt%)	Color
1A	278.5	4.4	73.1	22.5	1,245	3.7	Pink
1B	839.5	2.7	55.0	42.3	786	1.7	White
1C	975.7	2.2	55.7	42.1	1,378	1.2	White
1D	418.5	1.1	60.8	38.1	1,001	1.2	White

n, number of samples analyzed, mean results are given for sites 1, 2, and 3. A = 0–100 cm; B = 101–200 cm; C = 202–300; and D = 301–400.

frequented the most, contained the highest percentage of clay, fine silt, and sodium, and the lowest percentages of sand and iron (Table IIb).

XRD analysis detected (in order of abundance): quartz, illite, kaolinite, gibbsite, paragonite, siderite, halite, and magnesite. All soil samples had swelling properties, which implies that some form of smectite was present in the soils, but it was not detected in the analysis.

DISCUSSION

Time spent consuming soil at four sites and variation in soil composition provided insight into preference and function of geophagy in the Wildcliff troop of baboons. Below, we discuss our findings with respect to current hypotheses for the function(s) of geophagy.

Geophagy Alleviates Gastrointestinal Distress

Our data indicate the baboons consume soils containing high percentages of clay and fine silt and low percentages of sand. Soils from the preferred site contain the highest percentages of clay and fine silt and the lowest percentages of sand. This suggests that texture is an important factor in soil selection. Soils consumed by the baboons contain both expanding and nonexpanding clays, and we suggest that, based on particle size and large surface area, these clays provide some level of protection and detoxification inherent to clay. We do not suggest one specific form of GI distress occurred in this troop or was caused by one specific dietary item, but rather that the role of soil was multifunctional and that it protected the baboons via the adsorption of pathogens and dietary toxins, which could change over the course of time.

This interpretation is supported by studies conducted on several kinds of clay, which demonstrated that clay-rich soils have the ability to relieve GI distress and detoxify dietary toxins and pathogens [Gilardi et al., 1999; Gonzalez et al., 2004; Johns, 1986; Vermeer & Ferrell, 1985]. The degree of therapeutic benefit would vary in relation to clay particle morphology and adsorptive capacity. For example, Johns [1986] found that soils containing predominantly smectites and illites had adsorptive capacities approximately ten and three times, respectively, greater than kaolin.

We found no commonality in pH among all geophagy sites, but three of four sites were very strongly alkaline, and little time was spent feeding on soil from the fourth site, which was very strongly acidic. Based on pH, it was likely that the soils found at sites one, two, and four contained alkaline soluble salts and carbonate minerals, which could have acted as effective antacids [Wilson, 2003]. In addition, taste is defined partly by pH. Acidic soils are often described as ''sour'' and alkaline soils as ''sweet'' [Abrahams & Parsons, 1997]. The preference for alkaline soils could represent a taste preference and/or the soils' improved buffering capacity.

Geophagy-Supplemented Iron and Sodium

Our data indicated that clay color and mineral composition varied among the four geophagy sites, but the highest rates of soil consumption occurred where soil was white, and therefore iron concentrations were low. Whether or not baboons could detect gustatory changes imparted by iron is unknown, but if the baboons were selecting iron, the reddish hue imparted by the presence of iron could have acted as a primary or secondary stimulus to the baboons. However, soils pink in color were selected against. Therefore, our data do not support the hypothesis that soil was consumed for iron supplementation.

This interpretation of the data is supported by hematite's description as a large crystal that remains relatively stable even under acidic conditions [Wilson, 2003]. Our results would have been further supported if we had demonstrated whether or not minerals present in the soil were bioavailable to the baboons.

Our data indicated that this troop of baboons preferred ''salty'' soil. Few primate studies have suggested sodium acted as a stimulus for geophagy [Ganzhorn, 1987; Mahaney et al., 1993; Matsubayashi et al., 2007], but our data indicated that the baboons spent more time consuming soil that contained higher concentrations of sodium. We are uncertain whether this preference is owing to sodium deficiency or just a preference for salt in this troop.

The interpretation that salt was the primary stimulus for geophagy is not supported by the National Research Council, which states sodium requirements of 0.25–0.65% for omnivorous primates are met by most natural diets [2003]. Interestingly, baboons under experimental conditions have shown a preference for ''suprathreshold'' concentrations of sodium chloride that exceed dietary needs [Laska & Hernandez-Salazar, 2004].

Geophagy as an Antibiotic

No microbial studies were conducted on the soils consumed by the Wildcliff baboons. A growing body of literature suggests clay minerals may be a suitable alternative to antibiotics in the prevention of diarrheal diseases [Haydel et al., 2008; Ketch et al., 2001; Vondruskova et al., 2010; Williams et al., 2009; Williams & Haydel, 2010]. Future research should include microbial testing on geophagic soils.

Geophagy as a Famine Food

At no time during the study was food scarcity observed and amounts of soil consumed by the baboons were typically small. Despite the fact that soil has been and continues to be consumed by humans as a famine food [Abrahams, 2005; Aufreiter et al., 1997; Young et al., 2010], there is no evidence to suggest that NHP use soil as food. Therefore, our data do not support this hypothesis.

No Function Hypothesis

Our data indicated that the baboons did not consume all soils. In fact, when eating roots, corms, and tubers covered with soil containing high percentages of sand, baboons attempted to remove the soil from the plant before eating. The soils consumed showed a high degree of selectivity. Therefore, our data do not support the hypothesis that geophagy served no function.

Geophagy in Association With Pregnancy for NHP

Our data indicated that adult female baboons consumed significantly more soil than adult male and juvenile baboons, and that pregnant individuals consumed more soil than any other reproductive state. Statistically that difference, however, was not significant. We offer one potential explanation. The change in paracallosal skin coloration does not appear until the second week after the expected time of missed menstruation [Altman, 1970]. Before this color change, baboons in the early stages of pregnancy would have been classified as nonswelling. Therefore, it is conceivable that this overlap in classification could have falsely increased the representation of the nonswelling class's soil consumption time. In a fully habituated troop with all members identified and exact dates of birth known, back calculation could have been performed to follow all individuals through the entire pregnancy. The Wildcliff troop remained semi-habituated, so this was not possible in most cases. Based on soil properties, already discussed, these soils should have been effective at relieving GI distress and providing protection from dietary toxins.

Our interpretation of the data is supported by one animal study [Voigt et al., 2008] and human studies, which have shown that geophagy and pregnancy are highly associated [Hunter, 1973; Wiley & Katz, 1998; Young et al., 2011]. Nausea is difficult to detect not only in animals, but also in humans. We did make two potentially relevant observations of pregnant baboons vomiting and dry retching while at geophagy sites during this study. Additionally, during the breeding season at Cayo Santiago, pregnant rhesus macaques are said to frequently dry retch. Cayo researchers refer to this phenomenon as ''morning sickness'' (Jennifer Danzy, personal communication), and like the Wildcliff troop, these monkeys frequently consume soil [Knezevich, 1998; Mahaney et al., 1995b]. Whether or to what extent baboons and other NHP experience GI distress in association with pregnancy is unknown, but should be further investigated.

Human studies have suggested that soil consumption can negatively affect health by the ingestion of parasites, pathogens, and contaminated soil [Al-Rmalli et al., 2010; Kutalek et al., 2010; Luoba et al., 2005; Reid, 1992]. Future efforts should be given to understanding to what extent these negative aspects of geophagy affect health in NHP.

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