PRIMATES, 36(3): 323–333, July 1995

Geophagy Amongst Rhesus Macaques on Cayo Santiago, Puerto Rico

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ABSTRACT. Soil mining and eating (geophagy) behavior of rhesus macaques (*Macaca mulatta*) on Cayo Santiago, Puerto Rico, is described and assessed with respect to the chemical, geochemical, and mineralogical composition of the ingested materials. The samples forming the uneaten (control) and eaten (matrix and blocky) groups of soils come from the top and flanks of a marine terrace underlain with volcanic tuff on Cayo Santiago, off the east shore of Puerto Rico. Both the uneaten and geophagy samples were analyzed to determine particle size distributions, clay and primary mineralogy, and soil chemical and geochemical compositions. Primary minerals such as orthoclase and plagioclase feldspar in the clay fraction is higher in the control group than in the ingested samples. Both the control and matrix plus blocky samples have moderate to abundant amounts of kaolinite and halloysite (both silicon:aluminum = 1:1 type clay minerals) that may be important as a stimulus to geophagy behavior. The pH, total salts, and phosphorus levels in both the control and geophagy samples show considerable overlap with little clear indication of causal factors. Analysis of the geochemical data showed no clear cut elemental differences to suggest elemental supplementation as a possible explanation for mining and eating of tropical soil. It is possible that rhesus macaques ingest clay to obtain kaolinite/halloysite minerals which may alter the taste of their provided food, and may act as pharmaceutical agents to alleviate intestinal ailments such as diarrhea.

Key Words: Geophagy; *Macaca mulatta*.

INTRODUCTION

Geophagy in non-human primates in particular, and mammals in general, has stimulated considerable research in recent years with respect to its possible nutritional benefits (BELOVSKY, 1981; KREULEN & JAGER, 1984; KREULEN, 1985; MAHANEY, 1987, 1993; JOHNS, 1990; JOHNS & DUQUETTE, 1991; MAHANEY & HANCOCK, 1990; MAHANEY et al., 1990), medicinal function (JOHNS, 1990), and behavioral aspects (IZAWA, 1975; INOUE, 1987; ROGERS & KAPLAN, 1993). Several possible stimuli have been considered for this behavior. Geophagy has been regarded as a simple quest for salt (ROZIN, 1976; SINCLAIR, 1977; BELOVSKY, 1981; MLOSZEWSKI, 1983), as a fulfilment of mineral and trace element requirements (ROBBINS, 1983; ARTHUR & ALLDREDGE, 1979; WESTOBY, 1974), and/or as a means of using clay to adsorb toxins (OATES, 1978).

Soil eaten by non-human primates including gorillas (FOSSEY, 1983; WATTS, 1984), monkeys (IZAWA, 1975; HLADIK, 1977), chimpanzees (GOODALL, 1986), and orangutans (ROGERS & KAPLAN, 1993) ranges from only a fraction of dietary intake consumed occasionally (WATTS, 1984, African mountain gorilla) to significant amounts eaten over considerable periods of time (INOUE, 1987, Japanese macaques). Geophagy is thus a common but complex and variable behavior, both in its stimuli and its effects. While there are disadvantages to eating soil (KREULEN, 1985), there may be multiple benefits, though the stimulus for the behavior may be something specific. JOHNS and DUQUETTE (1991) have described the mixing of clays with acorn meal by humans as a means of alleviating the bitter taste of the meal. This practice may also absorb plant toxins into the clays, adsorb them onto clay surfaces, and/or prevent their absorption in the small intestine, permitting the use of the acorns as food without the detrimental effects of their toxins.

Rhesus macaques in Puerto Rico regularly extract and consume soil material from outcrops exposed on high marine terraces (SULTANA & MARRIOTT, 1982; MARRIOTT et al., 1990; MARRIOTT et al., 1993). The monkeys do not roll their food in the soil, but often have food in their cheek pouches when they eat soil. This behavior is often, but not exclusively associated with the consumption of monkey chow provided by the Research Center. Like Japanese macaques (INOUE, 1987), the monkeys eat soil on a daily basis. To examine possible stimuli for, and effects of, this behavior, we determined the physical, chemical, geochemical, and mineralogical composition of ingested soils. We anticipated that if mineral or chemical deficiencies exist in the chow provided for the macaques, we might find greater amounts of these deficient minerals or elements in the ingested soil relative to a control group of local soils. We assumed that the mined soils represented random sampling across a geological surface having nearly uniform mineralogy and chemistry. In this paper, we summarize a pattern of geophagy among rhesus macaques, and present results of the particle size, geochemical, chemical, and mineralogical analysis of the ingested soils. Possible reasons for and effects of this behavior are explored. Two elements, selenium and zinc, which are of nutritional importance to non-human primates (MCDOWELL, 1992), were not determined by our procedures.

FIELD AREA

LOCATION AND VEGETATION

Cayo Santiago is a small island (15.2 ha) located 1 km off the southeast coast of Puerto Rico at 18°09′N, 65°44′W. It is maintained as a rhesus monkey behavioral colony by the University of Puerto Rico's Caribbean Primate Research Center (see KESSLER & BERARD, 1989; RAWLINS & KESSLER, 1986). As shown in Figure 1, it has three distinct areas: Big Cay, Small Cay, and an alluvial lowland covered with mangrove (*Rhizophora mangle*) and coconut palm (*Cocos nucifera*). The natural vegetation on the island consists of grasses and scrubs. During the 1940's, attempts to introduce crop plants such as bananas, almonds, guavas, and limes met with limited success, and only the coconut palm survived. As many as 141 species of plants are eaten by rhesus macaques on the island (MARRIOTT, 1988; MARRIOTT et al., 1989; COWEN, 1990).

GEOLOGY AND CLIMATE

The geology of Cayo Santiago is of Lower Cretaceous and Pleistocene (and/or Recent) ages (BRIGGS, 1964), with Big Cay and Little Cay classified as part of the northeastern volcanic-plutonic subprovince (COX & BRIGGS, 1973). Lava breccia, tuff and tuffaceous sandstone, and siltstone outcrop here with limestone beds occurring sporadically in the

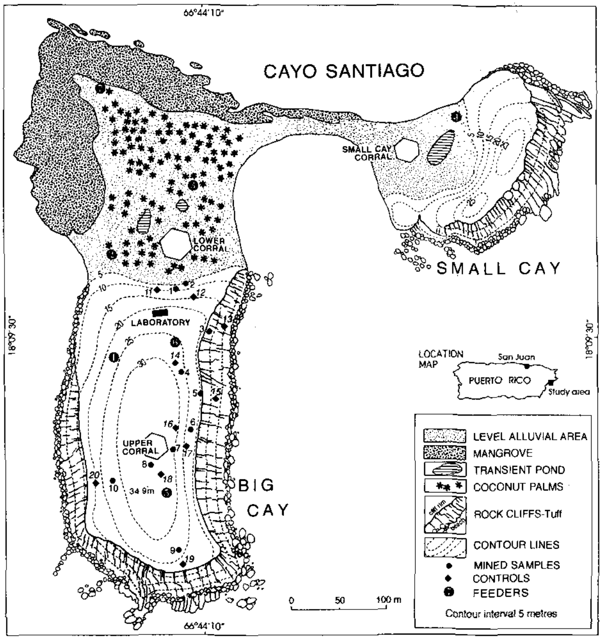

Fig. 1. Cayo Santiago, a small island of volcanic origin, consists of two small marine terraces (25 m and 35 m a.s.l.) off the coast of Puerto Rico. The locations of mined and control samples are shown on the map.

upper sequence (MONROE, 1980; COX & BRIGGS, 1973; BRIGGS & AKERS, 1965; KAYE, 1957). These extensively weathered rocks reflect the volcanic origin of the underwater mountain on which Puerto Rico is situated (WAGENHEIM, 1975). The alluvial/mangrove area consists of surficial deposits of beach and dune eolianites consisting primarily of calcite, quartz, and magnetite (BRIGGS, 1964; BRIGGS & AKERS, 1965). Both Big Cay and Small Cay are uplifted marine terraces.

Located within the Greater Antilles, Cayo Santiago's climate is predominantly affected by the northeasterly trade winds and the subtropical ocean current (KEMBALL, 1985). Mean annual temperature is approximately 25°C with daily extremes of 40° to 21°C. The rainfall is highest from May to October, occurring with the high sun.

METHODS

Samples of soil consumed by the monkeys were collected from ten different sites mined and frequented by the monkeys on the Big Cay (Fig. 1). Ten matching control samples were collected at a distance of 5 m from each mine in a randomly chosen direction (but within the terrace surface or flank).

The eaten samples contained blocks of fine-grained material within the matrix material, while the control samples consisted of non-blocky matrix material. So, samples were taken for chemical analysis both from blocky material and from the crumbly part of the eaten matrix materials (samples 1 – 10), as well as control samples from the uneaten materials (samples 11 – 20).

The collected samples were air dried, treated with 30% H_2O_2 to remove organic matter, and chemically dispersed with sodium pyrophosphate (except the blocky samples which had insufficient masses for particle size determinations), and mechanically dispersed by sonification to achieve deflocculation. Particle size analysis was carried out by wet sieving the sands and then calculating the individual fractions by dry sieving. The silt and clay fractions were calculated by hydrometer (DAY, 1965).

Phosphorous was determined with an autoanalyzer. Conductivity and pH were determined using 20 g samples of the <2 mm sample to 100 ml of distilled water (1:5 ratio).

All other elemental determinations were made by instrumental neutron activation analysis. For a description of this method see HANCOCK (1978, 1984) and MAHANEY et al. (1990).

The mineralogy of the <2 μm fraction was determined following procedures outlined by MAHANEY (1981, 1990) and WHITTIG (1965).

RESULTS AND DISCUSSION

PARTICLE SIZE

The particle size distributions of the sand (2000-63 μm), silt (63-2 μm), and clay (<2 μm) fractions are shown in Figure 2. In general, the control samples are more sandy (37 – 59%) than the ingested (matrix) group (11 – 37%). The silt content is slightly higher in the control group (ca. 8 – 45%) compared with the matrix groups (2 – 42%), and clay distributions show much higher percentages of clay in the matrix groups (52 – 88%) than does the control group (19 – 46%). The lower sand and higher clay fractions in the matrix group indicate that the rhesus macaques, from the sites available to them, show a clear preference for using clay-rich samples. The data also indicate that the macaques show a preference for finer-grained material with less silt and sand [even though there is some overlap: e.g. Upper

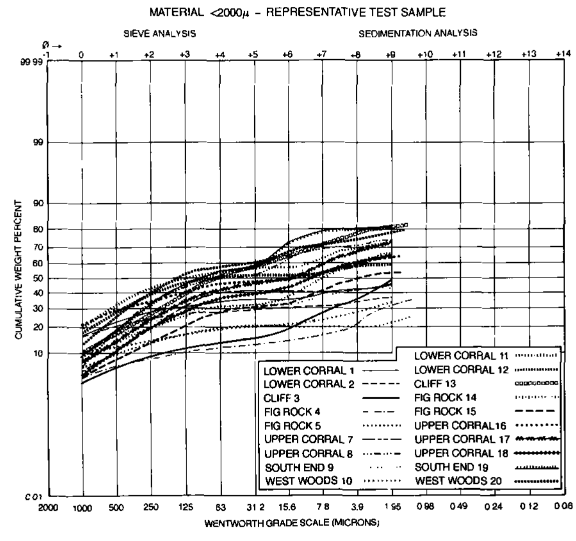

Fig. 2. Particle size distributions of control samples (not eaten) and geophagy samples ingested by rhesus macaques.

Corral 8 (Fig. 1 for location) falls within the control group of samples]. Upper Corral 8, infrequently used by the macaques, remained intact as a mine site. This mine may not have provided the preferred fine-grained material with the proper mineralogy, or perhaps the particle size composition changed over time, which led eventually to abandonment of the mine. The monkeys use, abandon, and create new mines elsewhere over time, as for example at Upper Corral 8, which is an infrequently used, but still intact, mine site.

The particle size trend is clear, however, in that the rhesus macaques prefer fine-grained sediment as a food supplement. The particle size was determined from the total bulk of the samples used by monkeys. We had insufficient sample sizes to carry out particle size analysis of the blocky peds (fine-grained soil structures or blocks) that the monkeys preferred to use as a food supplement. We did, however, have sufficient material to analyze the soil blocks for mineral composition.

MINERALOGY

The mineralogy (Table 1) of the <2 μm fraction was analyzed by XRD (WHITTIG, 1965)

Table 1. Mineralogy* of the <2 μm fraction of samples from Cayo Santiago, Puerto Rico.

	Clay minerals							Primary minerals		
Sample	K	H	I	S	I-S	V	Chl	Q	P	O
Blocky										
Lower corral 1	—	XX	X	—	—	—	—	tr	X	X
Lower corral 2	—	XXX	X	—	—	—	—	X	XX	X
Cliff 3	—	X	—	—	—	—	X	X	X	—
Fig rock 4	tr	XX	X	X	X	—	tr	X	X	tr
Fig rock 5	—	X	—	tr	—	—	tr	X	X	—
Upper corral 6	—	XXX	X	X	—	tr	—	X	X	—
Upper corral 7	—	XXX	X	X	—	tr	—	X	X	—
Upper corral 8	—	X	—	—	—	—	—	X	tr	—
South end 9	X	XX	tr	X	—	—	—	tr	tr	—
West wood 10	X	XXX	X	X	—	—	—	X	XX	X
Matrix										
Lower corral 1	—	XXX	XXX	—	—	—	—	XX	XXX	XX
Lower corral 2	XXX	XXX	XX	—	?	—	—	X	XXX	X
Cliff 3	—	XXX	X	tr	—	—	—	X	XXX	X
Fig rock 4	—	XXX	X	tr	—	—	—	X	XXX	XX
Fig rock 5	—	XXX	X	tr	—	—	—	X	X	X
Sample 6 (insufficient soil)										
Upper corral 7	XXX	XXX	X	X	X	—	—	X	X	XX
Upper corral 8	—	XXX	X	tr	X	—	—	XX	tr	X
South end 9	X	XXX	X	tr	X	—	—	X	X	X
West wood 10	XX	XXX	XX	tr	X	—	—	XX	XX	X
Uneaten										
Lower corral 11	—	XXX	XX	—	—	—	—	tr	XXX	X
Lower corral 12	XX	XXX	XX	—	—	—	—	X	XXX	X
Cliff 13	—	XX	X	XX	XX	—	—	X	X	X
Fig rock 14	—	XXX	X	tr	X	—	—	X	X	X
Fig rock 15	—	XX	X	tr	X	—	—	X	tr	X
Fig rock 16	—	XXX	XX	tr	tr	—	—	X	X	—
Fig rock 17	—	XX	X	—	X	—	—	X	X	tr
Upper corral 18	—	X	X	—	—	—	—	X	X	XX
South end 19	—	tr	—	—	—	—	—	X	X	—
West wood 20	tr	XXX	X	—	—	—	—	X	X	—

*Differentiation of clay and primary minerals. K: Kaolinite; H: halloysite; I: illite; S: smectite; I-S: illite-smectite; V: vermiculite; Chl: chlorite; Q: quartz; P: plagioclase; O: orthoclase; —: no detection; X: small amount; XX: moderate; XXX: abundant.

to determine if differences could be detected between the ingested samples (blocky and matrix) and the uneaten control group. Within the ingested sample groups, the primary minerals consist of quartz, plagioclase feldspar, and orthoclase, and show few trends. However, plagioclase feldspar and orthoclase are more abundant in the matrix group than in the blocky samples. The blocky samples, on the other hand, contain minor amounts of vermiculite and chlorite relative to the matrix group which do not contain these minerals. Also, smectite, an important 2:1 (silicon:aluminum = 2:1) expandable clay mineral found in the pharmaceutical Kaopectate, is more abundant in the blocky group compared with the matrix group. Illite and kaolinite are slightly higher in the matrix group than in the soil blocks.

All the minerals present within the matrix and blocky groups are also found in the uneaten control group with the exception of vermiculite and chlorite. Within the primary minerals, plagioclase feldspar is somewhat lower in the control group, but quartz and orthoclase have similar distributions. Smectite is present in trace quantities in the control group compared with the other two groups where it is more abundant. Illite is present in about the same quantity in all three groups and illite-smectite (randomly interstratified) is less abundant in the soil blocks.

Within the 1:1 (silicon:aluminum = 1:1) group of clay minerals, kaolinite, and halloysite are less prevalent in the uneaten control groups than in the other two groups. From a mineralogical assessment of the three groups of samples, several trends are noteworthy. The presence of chlorite in some of the ingested samples (samples 3, 4, and 5) may relate to the adsorption of toxins as discussed by OATES (1978) in his study of guereza monkeys, and examined at length by JOHNS (1990). Halloysite and kaolinite, when combined with small amounts of smectite, produce a mixture that bears a striking similarity to the pharmaceutical drug Kaopectate (see VERMEER & FERREL, 1985), and suggests that natural earths may be used by the macaques to alleviate gastrointestinal upsets and diarrhea. Indeed, previous research (KNEZEVICH, unpubl.) showed that though rhesus macaques have heavy parasite loads, they rarely have diarrhea. This suggests that frequent use of natural earths as a food supplement may maintain solid feces in the rhesus macaques.

The presence of uniform but low amounts of illite in the ingested samples may supply minor amounts of iron and potassium, if the gut pH is low enough to solubilize part of the ingested mineral. The primary minerals (quartz and plagioclase feldspar and orthoclase) probably pass through the gut without appreciable change. Kaolinite plus halloysite are relatively unaffected by ingestion; their main effect is likely to alleviate diarrhea. Halloysite may adsorb water much like smectite, aiding in solidification of the feces.

Given the small size of Cayo Santiago (Fig. 1), it may be that the rhesus macaques are ingesting samples at random from the marine terraces. If this is so, one would expect the control samples to vary little relative to the ingested samples. Sooner or later, as the dug caverns become larger, the macaques may ingest soil from the control group areas as well. If a Kaopectate-like substance is the stimulus for this behavior, it seems that the rhesus macaques have little chance of running out of suitable natural earths. Even the control group has sufficient halloysite and smectite to provide a similar effect.

SOIL CHEMISTRY

The soil color was estimated (Table 2) from soil color charts (OYAMA & TAKEHARA, 1970) to determine if it could be used to estimate the presence of organic matter or iron oxides and hydroxides. As shown in Table 2, the colors in the geophagy group are dominated by strong yellow brown hues ranging to 5YR 5/4. Only one sample (West Woods 10) has a 10YR color (weaker yellow red) within the geophagy group. The control group is dominantly 10YR with values from 5 to 7 and chromas from 2 to 6, which are generally yellowish brown to yellow orange colors. The colors indicate, in general, little organic matter in both groups of soil; however, the geophagy group colors suggest the presence of higher amounts of iron (both oxides and hydroxides). If soil color controls the selection of sites by the rhesus macaques, there may be a close correlation with selection of geophagic sites on Mount Kenya by African buffalo (MAHANEY, 1987, 1990) who show a preference for reddish-brown paleosols (old soils).

The pH distributions show a range from 5.2 to 7.0 in the geophagy group and 5.3 to 7.2 in the control group. However, the geophagy group has seven samples with pH <6.0, while the control group has only three samples with a pH <6.0. Thus, the geophagy group, despite some overlap with the control group, has a pH that is more acidic. In general, the higher acidity and redder colors (7.5 – 5YR) probably represent more intense leaching and higher amounts of iron oxides.

The electrical conductivity, shown in Table 2, was analyzed to determine if relative degrees of leaching had occurred in the two sample sets. The electrical conductivity approximates the presence of salts in a sample. The correlation with pH is clear; as alkalinity increases, the salts slowly increase. In most cases, the pH is at least moderately acidic and the conductivity is not high. The data indicate that some soils are possibly resupplied by salts (mainly chlorides) from the ocean and the pH remains acidic from the effects on the soil of the well-established vegetation and abundant precipitation. The underlying bedrock of basaltic composition probably does not supply much acidity to the soils.

The phosphorus distributions presented in Table 2 show considerable overlap between the matrix group and the control group. The concentration of phosphorus in the control group

Table 2. Physical and chemical soil analyses from Cayo Santiago, Puerto Rico.

Sample	Dry color	pH (1:5)	E.C. (S/cm^{-1})	Phosphorus (ppm)
Matrix				
Lower corral 1	I.S.	I.S.	I.S.	2.1
Lower corral 2	7.5YR 6/4	6.0	0.17	18.6
Cliff 3	7.5YR 6/6	5.2	0.17	3.5
Fig rock 4	10YR 5/4	5.0	0.17	25.6
Fig rock 5	7.5YR 6/3 & 5/3	5.8	0.17	4.3
Upper corral 6	5YR 5/4	5.2	0.22	2.5
Upper corral 7	7.5YR 5/3	7.0	0.67	198.0
Upper corral 8	7.5YR 5/3 & 5/4	6.2	0.29	335.0
South end 9	7.5YR 5/3 & 5/4	5.3	0.11	89.3
West woods 10	10YR 6/6	5.5	0.06	185.0
Uneaten				
Lower corral 11	10YR 5/6	7.2	0.14	22.0
Lower corral 12	10YR 6/4	5.8	0.10	15.2
Cliff 13	10YR 7/3	6.5	0.54	0.5
Fig rocks 14	10YR 5/3	6.3	0.14	10.7
Fig rocks 15	10YR 5/3	6.8	0.18	23.4
Upper corral 16	10YR 5/3	5.4	0.12	41.7
Upper corral 17	10YR 4/2 & 4/3	7.0	0.23	74.8
Upper corral 18	10YR 5/2	5.3	0.32	45.9
South end 19	10YR 5/3	6.7	0.18	95.7
West woods 20	10YR 5/2	6.2	0.08	36.4

I.S.: Insufficient sample.

is <100 ppm and many samples ($n=8$) are less than 50 ppm. While there are four samples in the matrix group with concentrations <10 ppm, three samples show phosphorus levels higher than 100 ppm. If phosphorus is an element lacking in macaque nutrition or dietary requirements, the available data indicate that the macaques may rectify a chemical imbalance in their food supply by adding these soils to their diet. However, there is no clear trend in this data set that could be used to prove a phosphorus deficient diet.

GEOCHEMISTRY

Table 3 shows the average results from the neutron activation analysis of soil samples from Cayo Santiago together with the group standard deviations at a 67% level of confidence. In this data set, <X±Y denotes that some detection limits were folded into the calculation of the elemental mean.

The first two columns of Table 3 give the analytical data for two different forms of the material that is eaten by the macaques. The blocky material represents the actual material

Table 3. Geochemistry of soils eaten by rhesus macaques, Cayo Santiago, Puerto Rico.

Element	Blocky samples 1 ~ 10	Matrix samples 1 – 10	Uneaten samples 11 – 20
Aluminum* %	11±3	11±2	12±3
Calcium %	1.0±0.9	1.0±0.6	1.7±0.6
Iron* %	7.6±0.8	7.6±0.7	9.1±1.8
Magnesium %	<0.8±0.4	<0.7±0.4	<0.7±0.5
Potassium %	<0.6±0.3	<0.7±0.3	<0.8±0.5
Sodium %	0.51±0.24	0.53±0.28	0.74±0.41
Titanium* %	<0.46±0.09	<0.49±0.07	<0.67±0.15
Antimony	1.8±2.8	2.0±3.4	1.1±1.1
Arsenic	<5.2±4.6	<5.8±5.1	<5.9±3.5
Barium	370±180	420±180	<450±210
Bromine	31±9	34±10	26±8
Caesium	<1.5±1.5	<1.5±1.5	<1.4±0.9
Cerium*	14±3	20±4	23±4
Chlorine	<700±1100	<800±1070	<500±310
Chromium	24±7	22±11	30±13
Cobalt	17±10	25±19	29±16
Europium*	1.2±0.3	1.3±0.3	1.5±0.2
Gallium	<26	<42	<42
Hafnium	2.0±0.4	2.1±0.5	2.2±0.7
Iodine	<47±28	<43±18	<28±7
Lanthanum*	6.2±0.7	8.5±2.4	10.1±1.8
Lutetium*	0.31±0.05	0.42±0.08	0.48±0.09
Manganese	600±390	860±500	1240±590
Neodymium	8±3	<10±3	13±2
Nickel	<44	<50	<60
Rubidium	28±11	28±13	35±10
Samarium	2.5±0.5	3.1±0.8	3.5±0.6
Scandium*	29±6	30±4	36±6
Strontium	<160±40	<130±40	<180±40
Tantalum	<0.22	<0.18	<0.20
Terbium	0.33±0.06	0.6±0.1	0.8±0.2
Thorium*	0.9±0.2	1.2±0.1	1.4±0.2
Uranium	<1.1	<1.4	<1.4
Vanadium*	240±40	250±40	310±80
Ytterbium*	2.2±0.4	2.5±0.4	3.0±0.7

All elemental concentrations in the larger list of elements are in ppm. *Groups better than ±20 to ±25%. <X±Y: Some detection limits were included in the calculation of the group mean.

eaten while the matrix material includes fine-powdered as well as blocky material. Within the elemental group precisions, as might be expected, there is essentially no difference between the mean elemental concentrations for the 35 elements sought in these two groups of samples. This implies that the soil samples are geochemically relatively homogeneous.

Relative to the data displayed in these two groups of samples, the group mean concentrations for the elements in the control material not eaten by the macaques (column three) is either equal to or greater than that found in the eaten material. Possible exceptions are the halogens iodine, bromine, and chlorine, all of which are, however, at or close to their detection limits.

Considering the dispersion of the total data set, as represented by the group precisions, these differences in the group mean values do not clearly separate the eaten from the not-eaten groups of soils. It is therefore unlikely that the monkeys obtained any benefit from the nutritionally important elements present in the eaten soils, unless the chemical form of the elements allowed them to be available for absorption.

CONCLUSIONS

Rhesus macaques on Cayo Santiago collect and consume soils. The macaques clearly show a preference for soils with less sand and silt and higher clay size material. The mineralogy of the mined samples shows little variation of primary minerals present between the matrix and blocky groups. Quartz, orthoclase, and plagioclase feldspar contents are small to moderate in amount within the control and matrix and blocky groups. The clay mineral distribution shows notable differences, especially with regard to the kaolinite-halloysite composition of the eaten material, which contains about the same amount of halloysite and more kaolinite. The ingested samples also have higher amounts of smectite resulting in a composition similar to Kaopectate. The stimulus for geophagy in rhesus macaques is unknown but may be to render their feed more palatable, as reported for humans mixing clays with food (JOHNS & DUQUETTE, 1991). Results of analysis of the clay mineralogy indicate that the rhesus macaques are using a natural earth which may act as a pharmaceutical agent to prevent or treat gastrointestinal upsets or diarrhea.

Acknowledgements. Soil chemical and mineral analysis was carried out in the Geomorphology and Pedology Laboratory at York University supported by an operating grant to W. C. MAHANEY from the NSERC. The New York State College of Veterinary Medicine, Cornell University, provided an International Veterinary Student Grant to M. KNEZEVICH during the summer of 1991. We thank J. BERARD of the Caribbean Primate Research Center for permission to conduct research and collect soil samples on Cayo Santiago. Research was supported by NIH Grant RR03640 to the Caribbean Primate Research Center, University of Puerto Rico Medical Sciences Campus. The Natural Sciences and Engineering Research Council of Canada provided an Infrastructure Grant to the SLOWPOKE Reactor Facility of the University of Toronto. JANET ALLIN (York University) drafted the illustrations.

REFERENCES

ARTHUR, W. J. & A. W. ALLDREDGE, 1979. Soil ingestion by mule deer in north-central Colorado. *J. Range Manage.*, 32: 62 – 71.

BELOVSKY, C., 1981. A possible population response of moose to sodium availability. *J. Mammal.*, 62: 631 – 633.

BRIGGS, R. P., 1964. Provisional geologic map of Puerto Rico and adjacent islands. U.S. Geological Survey Misc. Geol. Inventory Map I-392 (1:240,000).

——— & J. P. AKERS, 1965. Hydrogeologic map of Puerto Rico. U.S. Geological Survey Misc. Geol. Investigations scale 1:240,000.

COWEN, R., 1990. Medicine on the wild side. *Sci. News*, 138(18): 280–282.

COX, D. P. & R. P. BRIGGS, 1973. Metallogenic map of Puerto Rico. U.S. Geological Survey Map I-721 (1:240,000).

DAY, P. E., 1965. Particle fractionation and particle size analysis. In: *Methods of Soil Analysis*, C. A. BLACK (ed.), Amer. Soc. Agron., Madison, Wisconsin, pp. 545–567.

FOSSEY, D., 1983. *Gorillas in the Mist*. Houghton Mifflin, Boston.

GOODALL, J., 1986. *The Chimpanzees of Gombe*. Harvard Univ. Press, Cambridge, Massachusetts.

HANCOCK, R. G. V., 1978. Some aspects of the analyses of ancient artifacts by neutron activation analysis. *J. Int. Inst. of Conservation-Canadian Group*, 3: 21–27.

———, 1984. On the source of clay used for Cologne Roman pottery. *Archaeometry*, 26: 210–217.

HLADIK, C. M., 1977. A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In: *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*, T. H. CLUTTON-BROCK (ed.), Academic Press, London, pp. 324–353.

INOUE, M., 1987. Soil eating of Japanese macaques (*Macaca fuscata*) at Arashiyama, Kyoto. *Primate Res.*, 3: 103–111.

IZAWA, K., 1975. Foods and feeding behavior of monkeys in the upper Amazon basin. *Primates*, 16: 295–316.

JOHNS, T., 1990. *With Bitter Herbs They Shall Eat It: Chemical Ecology and the Origins of Human Diet and Medicine*. The Univ. of Arizona Press, Arizona.

——— & M. DUQUETTE, 1991. Detoxification and mineral supplementation as functions of geophagy. *Amer. J. Clin. Nutr.*, 53: 448–456.

KAYE, C. A., 1957. Notes on the structural geology of Puerto Rico. *Bull. Geol. Soc. Amer.*, 68: 103–118.

KEMBALL, W. G. (ed.), 1985. *The Canadian Oxford School Atlas* (5th ed.), Toronto, Oxford.

KESSLER, M. J. & J. D. BERARD, 1989. A brief description of the Cayo Santiago rhesus monkey colony. In: *Proceedings of the Meeting to Celebrate the 50th Anniversary of the Cayo Santiago Rhesus Monkey Colony*, M. J. KESSLER (ed.), P.R. *Hlth. Sci. J.*, 8: 55–59.

KREULEN, D. A., 1985. Lick use by large herbivores: a review of benefits and banes of soil consumption. *Mammal Rev.*, 15: 107–123.

——— & T. JAGER, 1984. The significance of soil ingestion in the utilization of arid rangelands by large herbivores with special reference to natural licks on the Kalahari pans. In: *Herbivore Nutrition in the Subtropics and Tropics*, F. M. C. GILCHRIST & R. I. MACKIE (eds.), The Science Press, Johannesburg, pp. 204–221.

MAHANEY, W. C., 1981. Paleoclimate reconstructed from paleosols: evidence from the Rocky Mountains and East Africa. In: *Quaternary Paleoclimate*, W. C. MAHANEY (ed.), Geobooks, Norwich, pp. 227–247.

———, 1987. Behaviour of the African buffalo on Mount Kenya. *Afr. J. Ecology*, 25: 199–202.

———, 1990. *Ice on the Equator*. Wm. Caxton, Ellison Bay, Wisconsin.

———, 1993. Scanning electron microscopy of earth mined and eaten by mountain gorillas in the Virunga Mountains, Rwanda. *Primates*, 34: 311–319.

——— & R. G. V. HANCOCK, 1990. Geochemistry of African buffalo (*Syncerus caffer caffer*) mining sites and dung on Mount Kenya, East Africa. *Mammalia*, 54: 25–32.

———, D. P. WATTS, & R. G. V. HANCOCK, 1990. Geophagia by mountain gorillas (*Gorilla gorilla beringei*) in the Virunga Mountains, Rwanda. *Primates*, 31: 113–120.

MARRIOTT, B. M., 1988. Time budgets of rhesus monkeys (*Macaca mulatta*) in a forest habitat in Nepal and on Cayo Santiago. In: *Ecology and Behaviour of Food-enhanced Primate Groups*, J. E. FA & C. H. SOUTHWICK (eds.), Alan R. Liss, New York, pp. 125–149.

———, E. PEARSON, J. ROEMER, & R. O. WOODBURY, 1993. Selection of a dietary supplements by free-ranging rhesus monkeys on Cayo Santiago. *Amer. J. Primatol.*, 30: 332. (Abstract)

———, J. ROEMER, & C. SULTANA, 1989. An overview of the food intake patterns of the Cayo Santiago rhesus monkeys (*Macaca mulatta*): report of a pilot study. In: *Proceedings of the Meeting to Celebrate the 50th Anniversary of the Cayo Santiago Rhesus Monkey Colony*, M. J. KESSLER (ed.), P.R. *Hlth. Sci. J.* 8: 87–94.

———, C. Sultana, & J. R. Roemer, 1990. Does soil serve as a condiment, a detoxicant or a mineral upplement for rhesus monkeys?: a comparison of results from Cayo Santiago and Nepal. *Amer. J. Primatol.*, 20: 210–211. (Abstract)

Mloszewski, M. J., 1983. *The Behaviour and Ecology of the African Buffalo.* Cambridge Univ. Press, London.

Monroe, W. H., 1980. Some tropical landforms of Puerto Rico. U.S. Geological Survey Project Paper, 1159.

Oates, J., 1978. Water-plant and soil consumption by guereza monkeys (*Colobus guereza*): a relationship with minerals and toxins in the diet? *Biotropica*, 10: 241–253.

Oyama, M. & H. Takehara, 1970. Revised Standard Soil Color Charts. Japan Research Council for Agriculture Forestry and Fisheries.

Rawlins, R. G. & M. J. Kessler (eds.), 1986. *The Cayo Santiago Macaques: History, Behaviour and Biology.* State Univ. of New York Press, Albany, New York.

Robbins, C. T., 1983. *Wildlife Feeding and Nutrition.* Academic Press, New York.

Rogers, L. J. & G. Kaplan, 1993. Koehler and tool use in orangutans. *Int. J. Comp. Psychol.*, 6(4): 234–241.

Rozin, P., 1976. The selection of food by rats, humans, and other animals. *Adv. Stud. Behav.*, 6: 21–76.

Sinclair, A. R. E., 1977. *The African Buffalo: A Study of Resource Limitation of Populations.* Univ. of Chicago Press, Chicago.

Sultana, C. J. & B. M. Marriott, 1982. Geophagia and related behaviour of rhesus monkeys (*Macaca mulatta*) on Cayo Santiago Island, Puerto Rico. *Int. J. Primatol.*, 3: 338.

Vermeer, D. E. & R. E. Ferrel, 1985. Nigerian geophagical clay: a traditional antidiarrheal pharmaceutical. *Science*, 227: 634–636.

Wagenheim, K., 1975. *Puerto Rico: A Profile* (2nd ed.), Praeger, New York.

Watts, D. P., 1984. Composition and variability of mountain gorilla diets in the Central Virungas. *Amer. J. Primatol.*, 7: 323–356.

Westoby, M., 1974. An analysis of diet selection by large generalist herbivores. *Amer. Naturalist*, 108: 290–304.

Whittig, L. D., 1965. X-ray diffraction techniques for mineral identification and mineralogical composition. In: *Methods of Soil Analysis*, C. A. Black (ed.), Amer. Soc. Agronomy, Madison, Wisconsin, pp. 671–696.

—— Received: *June 6, 1994*; Accepted: *November 14, 1994*

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