



REVIEW

Geophagy among primates: adaptive significance and ecological consequences

R. KRISHNAMANI* & WILLIAM C. MAHANEY†

*Division of Conservation Biology, Salim Ali Centre for Ornithology and Natural History

†Geomorphology and Pedology Laboratory, York University

*(Received 7 April 1999; initial acceptance 9 May 1999;
final acceptance 7 December 1999; MS. number: RV-12)*

We review geophagy, or soil ingestion, in primates. This behaviour is widespread and is presumed to be important to health and nutrition. Primates may engage in geophagy for one or a combination of reasons. Here we present, and make a preliminary assessment of, six nonexclusive hypotheses that may contribute to the prevalence of geophagy. Four hypotheses relate to geophagy in alleviating gastrointestinal disorders or upsets: (1) soils adsorb toxins such as phenolics and secondary metabolites; (2) soil ingestion has an antacid action and adjusts the gut pH; (3) soils act as an antidiarrhoeal agent; and (4) soils counteract the effects of endoparasites. Two hypotheses pertain to geophagy in supplementing minerals and/or elements: (5) soils supplement nutrient-poor diets and (6) soils provide extra iron at high altitudes. In addition to these hypotheses, geophagy may satiate olfactory senses, serve as a famine food and finally may have no function at all. We draw together a large body of information from various sources to assess these hypotheses and suggest some tests to understand the function of geophagy. Our review suggests that primates engage in geophagy for a number of reasons that are nonexclusive. We conclude that mineral supplementation, adsorption of toxins, treatment of diarrhoea and pH adjustment of the gut seem the most plausible reasons why primates engage in geophagy.

© 2000 The Association for the Study of Animal Behaviour

Primates consume a wide and complex variety of food items that vary temporally and spatially. Fruits, mature leaves, soft edible parts (such as flowers, leaf buds), seeds and invertebrates constitute the bulk of potential food items. The choice of a food item may be influenced by specific nutrients, energy needs, digestion inhibitors or toxins in the diet, constraints on the digestive system in removing inedible parts, competition, predation (e.g. Eisenberg et al. 1972; Milton 1980, 1984; McKey et al. 1981; Glander 1982; Altmann et al. 1987; Janson 1988) and gastrointestinal/stomach ailments (Wrangham & Nishida 1983; Huffman & Seifu 1989; Wrangham & Goodall 1989; Koshimizu et al. 1993). Despite the wide variety of food eaten, primates have also been observed to eat charcoal (Struhsaker et al. 1997),

dead wood (Struhsaker 1975) and soil. The deliberate ingestion of soil is termed geophagy or geophagia; soil consumption associated with eating insects and/or other things (as reported in Nishihara & Kuroda 1991) does not fall into this category.

Many primates have been reported eating soil, rock particles or clay (see Table 1) and 'the primate species concerned are usually selective with respect to the soil consumed and often concentrate on a few sites only' (Martin 1990, page 220). Of the 185 extant species of primates (Martin 1990) only 39 (21.1%) are reported to ingest soil, either in the wild or in captivity (Table 2). Of these, 28.2% are obligate folivores, 20.5% are obligate frugivores, 7.7% are frugivores/insectivores, 17.9% are folivores/frugivores and 25.6% are frugivores/omnivores. Similarly, only three of the 12 apes (25%), seven of the 36 prosimians (19.4%), 10 of the 64 New World monkeys (15.6%) and 19 of the 73 Old World monkeys (26%) are known to ingest soil (Table 3). This could be because primatologists have not done ecological studies on many primate species or have not observed geophagic

Correspondence: R. Krishnamani, Division of Conservation Biology, Salim Ali Centre for Ornithology and Natural History, Anaikatty PO, Coimbatore 641 108, India (email: liontailmac@hotmail.com). W. C. Mahaney is at the Geomorphology and Pedology Laboratory, Atkinson College, York University, 4700 Keele Street, North York, Ontario M3J 1P3, Canada.

Table 1. Primates reported to engage in geophagy

Species	Year of observation	Place	Soil type*	Soil analysis	Frequency†	Conclusion‡	Source
Prosimians							
Mongoose lemur, <i>Eulemur mongoz</i>	1994–1995	Anjamena, Madagascar (16°01'S, 45°54'E)	1	No	R	A§	Curtis & Zaramody 1998
Red-bellied lemur, <i>Eulemur rubriventer</i>	1988–1989	Ranomafana National Park, Madagascar (21°2'–21°25'S, 47°18'–47°37'E)	1	Yes	R	NA	Overdorff 1993
Red-fronted lemur, <i>Eulemur fulvus rufus</i>	1988–1989	Ranomafana National Park, Madagascar (21°2'–21°25'S, 47°18'–47°37'E)	1	Yes	R	NA	Overdorff 1993
Brown lemur, <i>Eulemur fulvus</i> (= <i>Lemur fulvus</i>) (semifree ranging)	1982–1984	Duke University Primate Center, Durham, U.S.A.	1	Yes	O	D	Ganzhorn 1987
Ring-tailed lemur, <i>Lemur catta</i> (semifree ranging)	1982–1984	Duke University Primate Center, Durham, U.S.A.	1	Yes	O	D	Ganzhorn 1987
Indri, <i>Indri indri</i>	1972–1973	Analamazoatra Forest, Madagascar	5	Yes	R	NA	Pollock 1975
Milne-Edward's sifaka, <i>Propithecus diadema edwardsi</i>	1991–1992	Ranomafana National Park, Madagascar (21°2'–21°25'S, 47°18'–47°37'E)	1	No	O	§	Hemingway 1998
Black-and-white ruffed lemur, <i>Varecia variegata variegata</i>	NA	NA	NA	NA	NA	NA	White 1989
New World monkeys							
Moustached tamarin, <i>Saguinus mystax</i>	1990	Estación Biológica Quebrada Blanco, Northern Peru. (4°40'S, 73°W)	1 and 2	Yes	O	D	Heymann & Hartmann 1991
Common marmoset, <i>Callithrix jacchus</i> (captive)	NA	NA	NA	NA	NA	NA	Bicca-Marquez & Calegato-Marquez 1994
Common woolly monkey, <i>Lagothrix lagotricha</i> (captive)	NA	NA	NA	NA	NA	NA	Bicca-Marquez & Calegato-Marquez 1994
Red howler monkey, <i>Alouatta seniculus</i>	1987–1990 1988–1990	La Mascarena National Park, Columbia (2°30'N, 74°30'W) Nourague Station, French Guiana (4°05'N, 52°40'W)	3 and 4 3	Yes No	R O	I A§	Izawa 1993; Hirabuki & Izawa 1990 Julliot & Sabatier 1993

Table 1. Continued

Species	Year of observation	Place	Soil type*	Soil analysis	Frequency†	Conclusion‡	Source
Black howler monkey, <i>A. caraya</i>	1989	Rio Grande do Sul State, Brazil (29°37'S, 56°17'W)	6	No	O	I§	Bicca-Marquez & Calegari-Marquez 1994
Red-handed howler monkey, <i>A. belzebul</i>	NA	NA	NA	NA	O	§	Bicca-Marquez & Calegari-Marquez 1994
Long-haired spider monkey, <i>Ateles belzebuth</i>	1987–1990	La Mascarena National Park, Columbia (2°30'N, 74°30'W)	3 and 4	Yes	R	I	Izawa 1993
	NA	NA	NA	NA	NA	NA	Izawa et al. 1979
Black-handed spider monkey, <i>A. geoffroyi</i>	NA	Tikal, Guatemala	NA	NA	NA	NA	Cant 1990
Masked titi monkey, <i>Callithecus personatus melanochir</i>	1992–1993	Estação Experimental Lemos Maia, Una, Bahia, Brazil (15°18'S, 39°06'W)	1, 2 and 9	Yes	O	A	Müller et al. 1997
Golden-faced saki, <i>Pithecia pithecia chnysocephala</i>	NA	NA	NA	NA	NA	NA	Setz & Enzweiler 1992
White-faced saki, <i>Pithecia pithecia pithecia</i>	1989–1990	Guri Lake Islands, Bolívar State, Venezuela (7°45'N, 62°52'W)	3	Yes	O	D§	Kinzey & Norconk 1993
Old World monkeys							
Chacma baboons, <i>Papio cynocephalus ursinus</i>	1958–1961	Southern Africa	NA	No	O	NA	Hall 1962
Mandrill, <i>Papio sphinx</i> (= <i>Mandrillus sphinx</i>) (free ranging)	1982–1983	Centre International de Recherche Medicales, Franeville, Gabon (1°40'S, 13°40'E)	NA	No	O	NA	Norris 1988
Red colobus monkey, <i>Procolobus badius tephrosceles</i> (= <i>Colobus badius tephrosceles</i>)	1969–1970	Gombe National Park, Tanzania (4°40'S, 29°38'E)	1	No	O	NA	Clutton-Brock 1972
Guereza monkey, <i>Colobus guereza</i>	1973–1974	Kibale National Park, Uganda (0°34'N, 30°21'E)	7	Yes	R	A/B	Oates 1978
Samango monkey, <i>Cercopithecus mitis labiatus</i>	1980–1984	Entabeni State Forest, Transvaal, South Africa (23°02'S, 30°17'E)	NA	No	NA	NA	Von dem Bussche & Van der Zee 1985
Japanese macaque, <i>Macaca fuscata</i>	1986–1987	Arashiyama and Takasakyama, Japan (35°N, 136°E and 33°N, 131°E)	1	Yes	R	D	Inoue 1987
	1986–1987	Arashiyama and Takasakyama, Japan (35°N, 136°E and 33°N, 131°E)	1	Yes	R	H	Mahaney et al. 1993

Table 1. Continued

Species	Year of observation	Place	Soil type*	Soil analysis	Frequency†	Conclusion‡	Source
Pigtailed macaque, <i>Macaca nemestrina</i>	1973–1975	Huay Kha Khaeng Game Sanctuary Thailand (15°30'N, 99°25'E)	8	Yes	O	D	Eudey 1978
Assamese macaque, <i>Macaca assamensis</i>	1973–1975	Huay Kha Khaeng Game Sanctuary Thailand (15°30'N, 99°25'E)	8	Yes	O	D	Eudey 1978
Rhesus macaque, <i>Macaca mulatta</i>	1973–1975	Huay Kha Khaeng Game Sanctuary, Thailand (15°30'N, 99°25'E)	8	Yes	O	D	Eudey 1978
	1967	Siwalik hills, Uttar Pradesh, India (30°20'N, 78°0'E)	3	Yes	O	NA	Lindburg 1977
	1980–1983	Tughlaqabad Fort, New Delhi, India (30°25'N, 78°76'E)	1 and 3	No	O	NA	Malik & Southwick 1987
	NA	NIHCE Laboratory, Dickerson, Maryland, U.S.A.	1	No	R	A	Gurian et al. 1992
	NA	Cayo Santiago, Puerto Rico (18°09'N, 65°45'W)	1	Yes	R	C and J	Mahaney et al. 1995b
	NA	Cayo Santiago, Puerto Rico (18°09'N, 65°45'W)	1	Yes	R	K	Knezevich 1998
Bonnet macaque, <i>Macaca radiata</i>	1991	Marakkanam Reserved Forest, Tamilnadu, India (12°11'N, 79°57'E)	3	No	O	§	Krishnamani 1994
	1991	Marakkanam Reserved Forest, Tamilnadu, India (12°11'N, 79°57'E)	3	Yes	O	J and C	J. Voros, W. C. Mahaney, M. W. Milner, R. Krishnamani, S. Aufreiter & R. G. V. Hancock, unpublished data
Toque macaque, <i>Macaca sinica</i>	1969–1970	Polonnaruwa Sanctuary, Sri Lanka (7°56'N, 81°00'E)	NA	NA	R	NA	Hladik & Gueguen 1974
Longtailed or crab-eating macaque, <i>Macaca fascicularis</i>	1973–1975	Huay Kha Khaeng Game Sanctuary, Thailand (15°30'N, 99°25'E)	8	Yes	O	D	Eudey 1978
	1974–1976	Kutai Nature Reserve, Borneo, Indonesia (0°35'N, 117°30'W)	1	Yes	O	D§	Wheatley 1980
Tibetan macaque, <i>Macaca thibetana</i>	1986	Mt Emei, China (29°33'N, 103°21'E)	NA	No	NA	NA	Zhao et al. 1991
Hybrid macaques, <i>M. mulatta</i> × <i>M. fuscata</i> × <i>M. fascicularis</i> × <i>M. thibetana</i> × <i>M. nemestrina</i>	1995	Kam Shan Park, Kowloon, Hong Kong, China (22°15'N, 113°30'E)	1	Yes	O	A, B and D	Bolton et al. 1998

Table 1. Continued

Species	Year of observation	Place	Soil type*	Soil analysis	Frequency†	Conclusion‡	Source
Hanuman or common langur, <i>Semnopithecus entellus</i> (= <i>Presbytis entellus</i>)	1931–1933	Bhambar Range, Gonda Forest Division, Uttar Pradesh, India (27°15'N, 82°10'E)	1	Yes	R	§	Caius & Chhapgar 1933
	1991–1992	Bardia National Park, Nepal (28°30'N, 81°15'E)	1	Yes	R	D	Moe 1993
	1981–1982	Kanha National Park, Madhya Pradesh, India	3	No	O	§	Newton 1992
Sri Lankan grey langur, <i>Semnopithecus entellus thersites</i> (= <i>P. entellus thersites</i>)	NA	NA	NA	NA	NA	NA	Ripley 1970
	1969–1970	Polonnaruwa Sanctuary, Sri Lanka (7°56'N, 81°00'E)	3	Yes	O	A	Hladik 1977a
Nilgiri langur, <i>Trachypithecus johnii</i> (= <i>Presbytis johnii</i>)	1966–1967	Nilgiri Hills, southern India (11°5'N, 76°5'E)	NA	No	O	A/B§	Poirier 1970
Capped langur, <i>T. pileatus</i> (= <i>Presbytis pileata</i>)	1986–1988	Madhupur National Park, Bangladesh	1	No	O	§	Stanford 1991
Purple-faced langur, <i>T. vetulus</i> (= <i>Presbytis senex</i>)	1969–1970	Polonnaruwa Sanctuary, Sri Lanka (7°56'N, 81°00'E)	3	Yes	O	A	Hladik 1977a
Red leaf monkey, <i>Presbytis rubicunda</i>	1980–1981	Sepilok Virgin Jungle Reserve, Malaysia (5°25'N, 117°30'E)	3	Yes	O	A, B, D	Davies & Baillie 1988
Banded langur, <i>P. melalophos</i>	NA	NA	NA	NA	NA	NA	Bennett 1983
Apes							
Mountain gorilla, <i>Gorilla gorilla beringei</i>	1959–1960	Virunga Volcanoes, Congo around (1°30'S, 29°30'E)	1¶	Yes	O	NA	Schaller 1963, 1965
	1967–1974	Visoke, Volcans National Park, Rwanda (1°30'S, 29°30'E)	1¶	No	R	NA	Fossey 1983
	1978–1979	Karisoke, Volcans National Park, Rwanda (1°30'S, 29°30'E)	1¶	No	R	§	Watts 1984
	1984–1985 probably	Karisoke, Volcans National Park, Rwanda (1°30'S, 29°30'E)	1	Yes	R	F	Mahaney et al. 1990
	NA	Visoke, Volcans National Park, Rwanda (1°30'S, 29°30'E)	1	Yes	R	C, J	Mahaney et al. 1995a
Western lowland gorilla, <i>Gorilla gorilla gorilla</i>	1983–1989	Lopé Reserve, Gabon (0°10'S, 11°35'E)	1	No	O	I§	Williamson et al. 1990

Table 1. Continued

Species	Year of observation	Place	Soil type*	Soil analysis	Frequency†	Conclusion‡	Source
Chimpanzee, <i>Pan troglodytes troglodytes</i>	1971–1972	CNRS Field Station, Ipassa, Gabon (0°20'N, 14°20'E)	3	Yes	R	A, E	Hladik 1977b; Hladik & Gueguen 1974
Chimpanzee, <i>Pan troglodytes schweinfurthii</i>	1961–1962	(Combe Stream Reserve) Gombe National Park, Tanzania (4°40'S, 29°38'E)	1	Yes	O	NA	Goodall 1965
	1972–1973	Gombe National Park, Tanzania (4°40'S, 29°38'E)	3	No	R	NA	Wrangham 1977
	1976–1978	KCRS, Mahale Mountains National Park, Tanzania (6°S, 30°E)	3	No	R	§	Uehara 1982; Nishihara & Uehara 1983
	1991	Mahale Mountains National Park, Tanzania (6°S, 30°E)	3	Yes	R	C and J	Mahaney et al. 1996b
	1996	Kibale National Park, Uganda (0°34'N, 30°21'E)	1	Yes	R	A, D and J	Mahaney et al. 1997
	1996	Mahale Mountains National Park, Tanzania (6°S, 30°E)	3	Yes	R	J and D§	Zippin 1998; Mahaney et al., in press
Sumatran orang-utan, <i>Pongo pygmaeus abelii</i>	1995–1996	Gunung Leuser National Park, Sumatra, Indonesia (3°41'N, 97°39'E)	NA	Yes	R	A, D and K	Stambolic-Robb 1997
Bornean orang-utan, <i>Pongo pygmaeus pygmaeus</i>	1995–1996	Sungai Rain Forest, Borneo, Indonesia (1°S, 117°E)	10	Yes	R	G and A§	Stambolic-Robb 1997

NA: Data not available.

*1: Forest floor; 2: mound of leaf-cutting ants; 3: termite mound; 4: 'Salado' (salty) soil; 5: base of upturned trees; 6: ovenbird, *Furnarius rufus* nest; 7: excavations at the base of live trees; 8: 'Pong' soil; 9: soil from decomposed tree trunks; 10: cicada mounds.

†R: Regularly; O: occasionally.

‡A: Absorption and/or adsorption of toxins; B: adjustment of gut pH and antacid action; C: anti-diarrhoeal agent; D: mineral/elemental supplementation; E: tactile sensation in mouth; F: altitudinal variation; G: visual and olfactory stimulus; H: no specific purpose; I: no single reason; J: gastrointestinal upset; K: to control parasitic load.

§Any hypothetical reason, no analysis made.

¶Volcanic soil.

Table 2. Classification of primates that engage in geophagy according to their feeding habits (modified after Eisenberg et al. 1972)

Frugivore/omnivore	Folivore/frugivore	Frugivore/insectivore	Folivore	Frugivore
<i>Macaca mulatta</i>	<i>Eulemur rubriventer</i>	<i>Saguinas mystax</i>	<i>Alouatta seniculus</i>	<i>Lemur catta</i>
<i>M. radiata</i>	<i>E. mongoz</i>	<i>Callithrix jacchus</i>	<i>A. caraya</i>	<i>Eulemur fulvus</i>
<i>M. fuscata</i>	<i>Propithecus diadema</i>	<i>Callicebus personatus</i>	<i>A. belzebul</i>	<i>Ateles geoffroyi</i>
<i>M. fascicularis</i>	<i>Indri indri</i>		<i>Semnopithecus entellus</i>	<i>A. belzebuth</i>
<i>M. assamensis</i>	<i>Varecia variegata</i>		<i>Trachypithecus johnii</i>	<i>Pithecia pithecia</i>
<i>M. sinica</i>	<i>Lagothrix lagotricha</i>		<i>T. pileatus</i>	<i>Papio sphinx</i>
<i>M. thibetana</i>	<i>Gorilla gorilla</i>		<i>T. vetulus</i>	<i>Cercopithecus mitis</i>
<i>M. nemestrina</i>			<i>Presbytis rubicunda</i>	<i>Pongo pygmaeus</i>
<i>Papio cynocephalus</i>			<i>P. melalophos</i>	
<i>Pan troglodytes</i>			<i>Procolobus badius</i>	
			<i>Colobus guereza</i>	

Table 3. Taxonomic classification of primates that engage in geophagy (adapted from Martin 1990)

Prosimians	New World monkeys		Old World monkeys		
	Cebidae	Callitrichidae	Colobinae	Cercopithecidae	Apes
<i>Lemur catta</i>	<i>Alouatta seniculus</i>	<i>Saguinas mystax</i>	<i>Semnopithecus entellus</i>	<i>Macaca mulatta</i>	<i>Gorilla gorilla</i>
<i>Eulemur fulvus</i>	<i>A. caraya</i>	<i>Callithrix jacchus</i>	<i>Trachypithecus johnii</i>	<i>M. radiata</i>	<i>Pan troglodytes</i>
<i>E. mongoz</i>	<i>A. belzebul</i>		<i>T. pileatus</i>	<i>M. assamensis</i>	<i>Pongo pygmaeus</i>
<i>E. rubriventer</i>	<i>Ateles geoffroyi</i>		<i>T. vetulus</i>	<i>M. fuscata</i>	
<i>Indri indri</i>	<i>A. belzebuth</i>		<i>Presbytis rubicunda</i>	<i>M. fascicularis</i>	
<i>Propithecus diadema</i>	<i>Lagothrix lagotricha</i>		<i>P. melalophos</i>	<i>M. sinica</i>	
<i>Varecia variegata</i>	<i>Callicebus personatus</i>		<i>Procolobus badius</i>	<i>M. nemestrina</i>	
	<i>Pithecia pithecia</i>		<i>Colobus guereza</i>	<i>M. thibetana</i>	
				<i>Papio sphinx</i>	
				<i>P. cynocephalus</i>	
				<i>Cercopithecus mitis</i>	
(7) 36	(8) 30	(2) 34	(8) 24	(11) 49	(3) 12

Numbers in parentheses are the geophagists and the numbers outside the parentheses are the extant primate species (the figures given are only a reasonable estimate and for a more recent account on primates, see Rowe 1996).

behaviour owing to difficult conditions, since most of the primates are in the tropics, and observing geophagy has always been a matter of serendipity. However, considering the growing scientific literature, it is only now that researchers are trying to understand the proximate and ultimate causes of geophagy. Primates are reported to ingest a variety of soils such as termite mound soils (24.3%), soil from the forest floor (36.5%), 'Salado' (salty) or 'Pong' (vernacular for mounds of earth in Thailand) soils (8.1%) and soil from the mounds of leaf-cutting ants and ovenbird nests (4.1%; Table 4).

Geophagy has also been reported in ungulates such as African elephants, *Loxodonta africana* (Weir 1969; Ruggiero & Fay 1994; Klaus et al. 1998), African buffaloes, *Synceros caffer* (Sinclair 1977; Mloszewski 1983; Mahaney 1987; Mahaney & Hancock 1990), mule deer, *Odocoileus hemionus* (Arthur & Alldredge 1979), Holstein cross cattle, *Bos primigenius* (Mahaney et al. 1996a), tapir, *Tapirus terrestris* (Izawa 1993), brocket deer, *Mazama* sp. (Izawa 1993) and pacas, *Agouti paca* (Izawa 1993). Geophagy has also been reported for birds (Izawa 1993; Diamond et al. 1999), reptiles, other mammals (Kreulen & Jager 1984) and herbivores in general (Kreulen 1985). Kreulen & Jager (1984) suggested that the unifying characteristic of those taxa

where geophagy had been reported is predominantly a herbivorous or omnivorous (e.g. pigs, primates) diet.

In this paper, we examine a number of nonexclusive hypotheses that might help explain geophagy in non-human primates, with some relevance to human beings. Detailed accounts on human geophagy have been published elsewhere (Laufer 1930; Halstead 1968; Danford 1982; Vermeer & Ferrell 1985; Aufreiter et al. 1997; for a more recent review on geophagy in human pregnancy see Wiley & Katz 1998).

HYPOTHESES

These hypotheses can be clustered into several categories. All indicate some medicinal value. First, geophagy is adaptive in alleviating gastrointestinal ailments. Second, it assists in mineral supplementation. Finally, it may also serve as a famine food, satiate sensory organs or may have no significance other than mere behavioural tradition. More than one of these explanations probably contributes to the prevalence of geophagy in primates. The relative importance of the various explanations may well vary in both time and space and is likely to be contingent on other ecological and behavioural factors. We present a number of hypotheses, assess the existing evidence for

Table 4. Classification of primates that engage in geophagy according to the type of soil they ingest

Soil from termite mound	'Salado' or 'Pong' soils	Forest floor	Soils from mounds*	Soils from tree bases†	Information not available
<i>Alouatta seniculus</i>	<i>Alouatta seniculus</i>	<i>Eulemur mongoz</i>	<i>Saguinas mystax</i>	<i>Indri indri</i>	<i>Propithecus diadema</i>
<i>Ateles belzebuth</i>	<i>Macaca mulatta</i>	<i>E. fulvus</i>	<i>Callicebus personatus</i>	<i>Colobus guereza</i>	<i>Varecia variegata</i>
<i>Pithecia pithecia</i>	<i>M. assamensis</i>	<i>E. rubriventer</i>	<i>Alouatta caraya</i>	<i>Callicebus personatus</i>	<i>Callithrix jacchus</i>
<i>Macaca radiata</i>	<i>M. nemestrina</i>	<i>Lemur catta</i>	<i>Pongo pygmaeus</i>		<i>Lagothrix lagotricha</i>
<i>M. mulatta</i>	<i>M. fascicularis</i>	<i>Propithecus diadema</i>			<i>Alouatta seniculus</i>
<i>M. sinica</i>		<i>Saguinas mystax</i>			<i>A. belzebuth</i>
<i>Semnopithecus entellus</i>		<i>Callicebus personatus</i>			<i>Ateles geoffroyi</i>
<i>Trachypithecus johnii</i>		<i>Macaca mulatta</i>			<i>A. belzebuth</i>
<i>Presbytis rubicunda</i>		<i>M. fuscata</i>			<i>Pithecia pithecia</i>
<i>Pan troglodytes</i>		<i>M. fascicularis</i>			<i>Papio sphinx</i>
		<i>Semnopithecus entellus</i>			<i>P. cynocephalus</i>
		<i>Trachypithecus pileatus</i>			<i>Cercopithecus mitis</i>
		<i>Procolobus badius</i>			<i>Macaca thibetana</i>
		<i>Gorilla gorilla</i>			<i>Trachypithecus johnii</i>
		<i>Pan troglodytes</i>			<i>Presbytis melalophos</i>
		Hybrid macaques			<i>Semnopithecus entellus</i>
					<i>Pongo pygmaeus</i>

*Soils from the mounds of leaf-cutting ants, ovenbird nest and cicada mounds.

†Soil from base of live and upturned trees and dead tree trunks.

each, and suggest some tests. We also provide a brief synopsis of some elementary information about geophagic soils (see Appendix). An ecological explanation for the prevalence of geophagy must encompass all the hypotheses put forward. The hypotheses discussed below are not exclusive, and their relative importance may vary seasonally, regionally and taxonomically.

Soil Adsorption of Toxins

Hladik (1977a, b) and Oates (1978) suggested that soils adsorb toxins including phenolics and secondary metabolites. Rainforest soils are poor in nutrients (Richards 1975) and Janzen (1974, 1975) surmised that the vegetation growing in these nutrient-poor soils protects its leaves with high concentrations of defensive secondary compounds (particularly phenolics) and that this chemical defence is likely to be related to the length of dry seasons and successional stages. Places from where geophagy has been reported support this hypothesis (Hladik 1977a, b; Oates 1978; Julliot & Sabatier 1993) as they are all in tropical rainforests, barring one site (Polannurwa, where Hladik 1977a studied the leaf-eating monkeys of Sri Lanka, which is in a tropical dry evergreen forest and has a prolonged dry season, Dittus 1985).

Rainforest herbivores, such as the leaf-eating primates, sometimes encounter high concentrations of phenolics (such as flavanoids, tannins, etc.) and toxic secondary compounds such as alkaloids while feeding (Freeland & Janzen 1974). Leaf-eating primates have symbiotic bacteria in their foregut that detoxify most of the plant toxins and feed deterrents that might cause gastrointestinal upsets. These leaf-eating monkeys sometimes circumvent this problem, either by avoiding mature leaves that are high in secondary compounds and choosing leaves of colonizing deciduous tree species (Oates 1977),

or by eating more seeds than leaves (e.g. black colobus monkey, *Colobus satanus*: McKey 1978).

Tannins, as soluble phenolics, are ancient, widespread and very successful generalized plant defence compounds (Swain 1979) occurring in about 87% of rainforest woody plants (Rhoades & Cates 1976). Although tannins are sometimes useful to these monkeys (Oates 1977, page 314), they inhibit protein absorption (Feeny 1969; Gurian et al. 1992).

The Pomo Indians of California and the Zuni people of New Mexico ingest earth along with their food. This is probably to counteract or reduce the acidity and astringency of the various foods they eat (Laufer 1930), since 'bitterness can be an indication of the presence of alkaloids and astringency of the presence of tannins' (Oates 1978, page 251; Bate-Smith 1972). Clays that contain kaolin are thought to adsorb toxins and promote their excretion (Jones 1957; Daykin 1960). Gurian et al. (1992) showed that rhesus monkeys, *Macaca mulatta*, feeding on vegetation with high concentrations of tannins also consume high amounts of clay-rich kaolinitic soil.

This hypothesis offers a reasonable explanation for the consumption of soil. A test for it would be to show that the soil from where geophagy has been reported adsorbs phenolics such as tannins at least in vivo. This hypothesis may explain charcoal consumption by the Zanzibar red colobus monkeys, *Procolobus kirkii*, for which Cooney & Struhsaker (1997) showed that charcoal consumption counteracts the toxic effect of phenolics.

Soil as an Antacid

When food is fermented anaerobically in the enlarged forestomachs of leaf monkeys, large quantities of volatile fatty acids are produced. This in turn decreases the stomach pH thereby causing 'acidosis' which can be fatal

(Goltenboth 1976). Ingestion of clay helps adsorb organic molecules, such as fatty acids, and because of their buffering action, it helps adjust the gastric pH and acts as an efficient antacid. Daykin (1960) listed kaolin as an effective antacid in veterinary practice. In field studies where the soils (clay) eaten by monkeys have been shown to have an antacid action (Poirier 1970; Oates 1978; Davies & Baillie 1988), however, the soils have not contained kaolin, although the antacid properties of kaolin were mentioned by Oates (1978) and Mahaney et al. (1997).

The forestomach of these folivores must be at a high pH to sustain their symbiotic bacteria. This pH generally varies from 5.4 to 6.9 in wild ruminants and is dependent on the balance between fermentation rate and the production of volatile fatty acids (Robbins 1983). During fermentation the stomach pH tends to fall as volatile fatty acids are produced. The ingested clay may enhance the buffering action of the stomach secretions or counteract the effects of particularly acid food (Oates 1978). The soil ingredients may also act as a catalyst in increasing the fermentation rates and reducing the production of volatile fatty acids.

Pepto-Bismol (Proctor & Gamble Co., Cincinnati, Ohio, U.S.A.) is regularly used as an antacid to quell stomach upsets and to control diarrhoea amongst rehabilitated orang-utans, *Pongo pygmaeus* (A. Russon, personal communication). The active ingredients in Pepto-Bismol include bismuth subsalicylate, parabens and sodium. It is not known, however, whether bismuth-rich natural earths containing nontronitic clay minerals (Fe-rich smectite) are available to orang-utans and achieve a similar result in nature.

To assess this hypothesis, we need to investigate whether the soil controls stomach acidity directly by regulating the production of volatile fatty acids or by affecting the symbiotic bacteria present. Future studies should test for any microbial activity present in the soil that may enhance the rate of anaerobic fermentation. The role of soil pH in controlling stomach acidity should also be investigated.

Soil as an Antidiarrhoeal Agent

Davies & Baillie (1988) stated that in many reports of mammalian geophagy the ingested material contains a high amount of 1:1 (Si:Al=1:1) lattice kaolinitic and/or metahalloysitic minerals as the main component of the clay fraction. This is particularly the case with human geophagy (Aufreiter et al. 1997), where kaolin and kaolin derivatives such as halloysite and metahalloysite preparations are recognized as effective pharmaceuticals countering most bowel and gastric disorders. Vermeer & Ferrell (1985), Mahaney (1993) and Aufreiter et al. (1997) listed kaolin and metahalloysite as effective antidiarrhoeal agents for both human and nonhuman primates. Hence, clay with halloysite and metahalloysite minerals present in it probably acts very much like kaolinite when eaten (Mahaney et al. 1995b, 1996b, 1997). Kaolinite is the main ingredient in Kaopectate (Pharmacia & Upjohn, Peapack, New Jersey, U.S.A.), and would make the dung firm if primates have diarrhoea.

Mahaney et al. (1995a) suggested that the weathered regolith consumed by mountain gorillas, *Gorilla gorilla beringei*, at Visoke, Rwanda, controls diarrhoea. Western lowland gorillas, *Gorilla gorilla gorilla*, are frugivores (Rogers et al. 1990) whereas allopatric mountain gorillas are predominantly folivores (Fossey & Harcourt 1977), and being monogastric primates they do not have any specialized adaptation in their stomach for detoxifying the plant toxins in their diet (Bramble 1972, cited in Fossey & Harcourt 1977). Hence mountain gorillas suffer from diarrhoea in the dry season when there is a shift in their feeding habits and their diet is dominated by bamboo shoots, *Arundinaria alpina*. In the mountain gorillas, geophagy is a seasonal phenomenon, coinciding with the dry season (Mahaney et al. 1995a).

A reasonable test of this hypothesis would be to test soil thought to control diarrhoea on laboratory primates.

Soil and Endoparasites

In a study on the rhesus macaques of Cayo Santiago, Knezevich (1998) found that regular ingestion of soil counteracts endoparasitic infections and thereby increases their fitness. Bicca-Marques & Calegario-Marques (1994) also observed this in black howler monkeys, *Alouatta caraya*, and mentioned endoparasites in red howler monkeys, *Alouatta seniculus*. Nearly 89% of the monkeys in Knezevich's (1998) study group had one or more species of enteric parasites. Regular ingestion of clayey soils may have led to homeostasis with the monkeys' parasitic loads. 'The mechanism whereby these animals have achieved this equilibrium is unknown. Presumably, immunologic and other mediators are at work to ameliorate the potentially damaging or life-threatening effects of these heavy parasite loads' (Knezevich 1998, page 79). Here again, highly adsorptive clay minerals, kaolinite and smectite, have been found to benefit the macaques. Ingestion of these natural clays may be instrumental in preventing the symptomatology and subsequent debility that would generally be associated with such heavy parasitic loads. This hypothesis, like the previous one, can be tested in the laboratory on primates found with enteric parasites.

Mineral and/or Elemental Supplementation

Mineral supplementation has been proposed by the majority of researchers who have observed geophagy in primates (Eudey 1978; Wheatley 1980; Inoue 1987; Davies & Baillie 1988; Heymann & Hartmann 1991). Chemical elements are an extremely diverse group of nutrients that have many essential functions. Deficiencies and imbalances of minerals are well recognized as important determinants of animal physiology, fertility, productivity and mortality (Robbins 1983). Minerals can be divided into macroelements, microelements and trace elements. The majority of the macroelements are present in the diet of primates but mineral deficiencies could arise if the primates are forced to feed on nutrient-poor diets (see Oates 1978). Microelements

and trace elements are essential as catalysts in cellular enzyme systems and for synthesis of DNA and RNA (for more information on trace elements see Underwood 1977).

Soils analysed for their mineral content include termite mounds (Davies & Baillie 1988; Mahaney et al. 1996b), forest floor (Wheatley 1980; Inoue 1987), mounds of leaf-cutting ants (Heymann & Hartmann 1991) and 'pong' soils (Eudey 1978). Termite mound soils contain high concentrations of certain nutrients such as calcium, magnesium, potassium and phosphorus (Wood & Sands 1978; Mahaney et al. 1996b). This may come about by microbial mineralization of organic matter from termite foraging (Pomeroy 1983), or the presence of antibiotics (Ketch 1998). The high nutrient status of termite mounds can be attributed to the evaporation of soil moisture from the mound surface, resulting in a high concentration of salts or carbonates (Hesse 1955; Weir 1973). Salick et al. (1983) suggested that termite mounds represent localized concentrations of nutrients in an intensively leached environment, although excessive leaching will remove most soluble compounds. Although nothing is known about 'pong' soils, mounds constructed by leaf-cutting ants have been found to have high concentrations of nutrients like the termitaria (Petal 1978). Hence, it is possible that primates eat earth that is rich in nutrients provided either by ants or termites.

Recent analyses of termite mound material from Mahale, Tanzania, which is regularly ingested by chimpanzees, *Pan troglodytes schweinfurthii* (Mahaney et al. 1996b, in press; Zippin 1998), show a clay mineral composition of metahalloysite and smectite. The composition of this material is almost identical to that of Kaopectate (Mahaney et al. 1995b), with well-crystallized 1:1 (Si:Al=1:1) metahalloysite and somewhat less well-crystallized smectite (mainly montmorillonite as a 2:1 (Si:Al=2:1) layer clay). This clay mineralogy is also similar to earth ingested by mountain gorillas in the Virunga Mountains of Rwanda (Mahaney et al. 1990) and by rhesus macaques in Puerto Rico (Mahaney et al. 1995b).

To test this hypothesis it is necessary to analyse the mineral contents of the soils of the surrounding area, the plant parts the primates eat and the water they drink. Since physiological condition (e.g. if the primate is sick, pregnant, convalescing, lactating, etc.) can affect the requirement for chemical elements, one would need to know this as well.

Altitudinal Variation

Mahaney et al. (1990) proposed this hypothesis, which also suggests a form of mineral/element supplementation, after analysing the geophagic sites of mountain gorillas. The ingested soil contained elevated concentrations of sodium, iron and bromine. Iron is the element present in haemoglobin. Hence, humans living at high altitude need iron-rich food to increase erythrocytes in the blood (Stickney & van Lier 1953; Matthews 1954). For the same reason Mahaney (1993) attributed iron deficiency to gorillas that live at 2400–3500 m above sea level. Iron depletion may explain geophagy in gorillas

living at higher altitudes, especially since they range across several hundred to over 1000 m elevation over short (24-h) periods.

The hypothesis of iron deficiency lends credence to the geophagic behaviour of African buffaloes ranging between 2800 and 3050 m on Mount Kenya. Again iron, in the soil consumed by buffalo, appears to be the sole reason for this behaviour (Mahaney 1987; Mahaney & Hancock 1990).

To test this hypothesis one needs to know if other animals ranging at a similar altitude engage in geophagy, the role iron might play in this behaviour and whether iron figures prominently in the soil analyses. Thorough phytochemical (of the surrounding vegetation) and water analyses are also essential to determine any chemical shortfall that might be taken up by geophagy. Geophagy can 'be either a useful source of iron or a contributing factor to anemia in wild animals, depending on soil iron content and chelating capacity of soil clay' (Robbins 1983, page 53).

Other Hypotheses

Mahaney et al. (1993) proposed that, in some cases, soil ingestion may not serve any purpose at all. They found that soil eating by Japanese macaques, *Macaca fuscata*, did not seem to fit any of the hitherto-mentioned hypotheses. However, there may be a reason for their geophagy that we do not yet know, or the ingestion may result from a behavioural tradition where one eats soil because others do it. Further work with Japanese macaques is required to determine the stimulus or stimuli for their geophagic behaviour.

In a study of soil eating by *Alouatta* and *Ateles* in Colombia (Izawa 1993), the elemental composition, including Ca, Mg, K, Na and P, provided no clear-cut stimulus for geophagy. However, water from three nearby geophagy sites had high electrical conductivity with high Na but normal Cl, which removes sodium chloride as a stimulus. While the elemental composition proved inconclusive, the clay mineral composition, if known, might have provided positive results. We recommend analysing both the elemental and mineralogical composition of ingested materials in future studies.

Soil ingestion related to its smell, as a hypothesis, has not been documented in the geophagy literature, but primates may respond to a stimulus or stimuli of the olfactory nerve (see Stambolic-Robb 1997 for orangutans). The smell of wet soils, soils rich in clay, or containing salts or lime, and/or organic matter may play a role in primate geophagy. The presence of organic matter in organically bound iron may provide an olfactory stimulation that leads primates to soluble iron (a working hypothesis that should be considered given that gorillas are likely to require increased iron to supplement deficiencies in haemoglobin, Mahaney et al. 1990).

While some animals respond to the smell of salt (Mloszewski 1983), sodium chloride has never been shown to be a stimulus in primate geophagy. Johns (1990) postulated a range of olfactory sensitivity in

Table 5. Classification of primates that engage in geophagy according to the hypotheses mentioned in the text

Mineral/elemental supplementation	Adjustment of gut pH and antacid action	Adsorption of toxins	Antidiarrhoeal agent	Other reasons*	Information not available
<i>Lemur catta</i>	<i>Colobus guereza</i>	<i>Callicebus personatus</i>	<i>Macaca radiata</i>	<i>Ateles belzebuth</i>	<i>Eulemur mongoz</i>
<i>Eulemur fulvus</i>	<i>Presbytis rubicunda</i>	<i>Colobus guereza</i>	<i>M. mulatta</i>	<i>Alouatta seniculus</i>	<i>E. fulvus</i>
<i>Saguinas mystax</i>	<i>Trachypithecus johnii</i>	<i>Macaca mulatta</i>	<i>Pan troglodytes</i>	<i>Macaca mulatta</i>	<i>E. rubriventer</i>
<i>Pithecia pithecia</i>	Hybrid macaques	<i>Semnopithecus entellus</i>	<i>Gorilla gorilla</i>	<i>M. radiata</i>	<i>Propithecus diadema</i>
<i>Macaca fuscata</i>		<i>Trachypithecus vetulus</i>		<i>M. fuscata</i>	<i>Indri indri</i>
<i>M. nemestrina</i>		<i>Presbytis rubicunda</i>		<i>Gorilla gorilla</i>	<i>Varecia variegata</i>
<i>M. assamensis</i>		<i>Pan troglodytes</i>		<i>Pan troglodytes</i>	<i>Callithrix jacchus</i>
<i>M. fascicularis</i>		<i>Pongo pymaeus</i>			<i>Lagothrix lagotricha</i>
<i>M. mulatta</i>		Hybrid macaques			<i>Alouatta seniculus</i>
<i>Semnopithecus entellus</i>					<i>A. caraya</i>
<i>Presbytis rubicunda</i>					<i>A. belzebul</i>
<i>Pan troglodytes</i>					<i>Ateles belzebuth</i>
Hybrid macaques					<i>A. geoffroyi</i>
					<i>Pithecia pithecia</i>
					<i>Papio cynocephalus</i>
					<i>P. sphinx</i>
					<i>Macaca mulatta</i>
					<i>Pan troglodytes</i>
					<i>Gorilla gorilla</i>
					<i>Trachypithecus johnii</i>
					<i>T. pileatus</i>
					<i>Presbytis melalophos</i>
					<i>Semnopithecus entellus</i>
					<i>Procolobus badius</i>
					<i>Pan troglodytes</i>
					<i>Gorilla gorilla</i>

*Other reasons include visual and olfactory stimulus, to control parasitic load and no specific purpose.

animals including 'sweet, salty, sour and bitter' smells that individual species may be able to recognize.

Nonhuman primates ingesting toxic plant material may seek specific clay minerals by olfactory sensation in order to rid their gastrointestinal tract of harmful plant compounds, for example, chimpanzees consume certain clays on a daily basis (Hladik & Gueguen 1974; Wrangham 1977; Mahaney et al. 1997). While it is difficult to prove that stimulation of the olfactory nerve plays a role in locating specific clays, it is a possibility and this hypothesis should be tested experimentally. An example of the importance of smell and taste for specific clay minerals comes also from potters who routinely smell and taste clays to judge their suitability for making pots (R. G. V. Hancock, personal communication).

In addition to these hypotheses, soils have been used as a famine food by human beings. While there is no documented evidence for this hypothesis among non-human primates, there is abundant evidence among humans (Aufreiter et al. 1997). Clays of various kinds are eaten by humans in some areas (Johns 1990). Geophagy among humans is an ancient cultural practice (Hunter & de Kleine 1984; Johns & Duquette 1991) and proliferates in subsistence cultural groups when food is scarce and when human beings are pregnant (Wiley & Katz 1998). Across much of West Africa, humans have been known to eat kaolinitic clay, partly as a food supplement, and to relieve gastrointestinal malaises (see above).

In parts of Africa and in China, humans have eaten earth as a famine food or as a supplement for loss of iron. Some soils tested by humans as famine foods have been

discarded because of acrid taste or stomach upsets, which may be linked to low levels of arsenic at concentrations of 20 ppm (S. Aufreiter, personal communication). Most famine soil food contains Fe, Mn, Cr, K, Ca and Na (with minimal Cl), which, if in the proper form, could act as mineral/elemental supplements to an undernourished diet. Although these observations do not examine the question of soil as food, they indicate that some form of nutritional benefits might be obtained.

CONCLUSIONS

Our review suggests that primates engage in geophagy for a number of reasons that are nonexclusive. From the available literature we may safely conclude that mineral supplementation (19.5%), adsorption of toxins (12.2%), control of diarrhoea (4.9%) and pH adjustment of the gut (4.9%) seem the most plausible reasons why primates indulge in geophagy, as many studies point to these (Table 5). There are no data to suggest that primates consuming soil are pregnant or lactating and convalescing, but this occurs in human beings (Kreulen & Jager 1984, page 206; Wiley & Katz 1998). Also we do not have enough data to show if there is a considerable difference in soil ingestion between the various age/sex classes in primates. For some primates geophagy may be a traditional behavioural activity and they may eat soil often while others do so infrequently. The geochemical components of the soil or clay composition may have a therapeutic benefit, which the primates are exploiting,

even though we have not been able to demonstrate the importance of many trace elements.

Glander (1994) suggested that many nonhuman primates engage in the selection and use of different plants to cure malaises of one kind or another. In recent articles Mahaney et al. (1995b, 1996b) have suggested this might extend to experimenting with soils to try to cure intestinal ailments, or as useful antacids (Mahaney et al. 1996a). Few studies have analysed the microbial aspects of geophagy (Ketch 1998), although soil often harbours fungi and bacteria. These may have a bacteriostatic or bactericidal effect on the consumer or the fungi may produce acids to inhibit the growth of bacteria: 'bentonite and zeolite clays in the diet of rats have been shown to protect (them) against certain mycotoxins by adsorption' (Carson & Smith 1983 and Smith 1980 cited in Kreulen 1985, page 117). So far this sort of beneficial effect has not been proved in primates. Research is needed to look at the microbiological aspects of soils ingested by nonhuman primates to determine whether drug-related stimuli might explain geophagic behaviour.

With respect to termite mound soils, we need analyses of a cross-section of the mound including: (1) the termite tunnels; (2) earth between tunnels; (3) organic colloids in termite mounds that may be related to compounds excreted by chimpanzees in their uric acid (anticarcinogens; L. Thompson, personal communication); (4) presence of the soil microflora (bacteria and fungi) that may act as a pharmaceutical agent; and (5) elemental chemical and mineral stimuli. Moreover, to understand geophagy amongst primates it is necessary to analyse control samples of what they do not eat, that is, the refuse. In most cases what they eat is part of a soil profile or geological section (vertical slice of the skin of the earth with maximum and minimum ages). The layers (horizons) of ingested earth need to be accurately described, collected as multiple samples and analysed as replicates to form a valid population of biological, chemical and mineral data. The earth from younger (top) and older (bottom) beds of a geological section/profile from the ingested sample needs to be analysed and collected as control samples. It is only with physical, chemical, mineralogical and microbial analyses of multiple samples of ingested earth, along with an adequate number of control samples, that we can gain insight into the reasons for geophagic behaviour.

As in all questions dealing with ecological contributors to the prevalence of geophagy, a real problem lies in the variation of the proposed selective pressures. Geophagy, for example, may be expressed only by some individuals, or by some species, at some times or places, and yet may still be important; and we can seldom know whether current ecological pressures operated in the same way at some time in the distant past. However, our present state of knowledge remains distant from these confines. Detailed observations of what is eaten and how primates obtain the samples are required, to understand the behaviour. In addition to these, we also need a complete phytochemical analysis of the surrounding vegetation. A thorough investigation of the physical well-being of the primate would complement the investigation.

It is unlikely that the prevalence of geophagy has a single explanation and a variety of possibilities must be borne in mind. Naturalists have known of the prevalence of geophagy for a number of years, but only now are wildlife biologists trying to understand this phenomenon. Yet, progress in understanding such a conspicuous ecological question has been small. More specific studies are needed to understand geophagy; until then we can only document it and present reasonable estimates of possible stimuli in primates. Future research requires interdisciplinary efforts between soil and behavioural scientists, with well-designed research projects focusing on a detailed study of the environment where geophagy is undertaken. Our goal has been to focus attention in a way that may encourage research of the type needed to begin to answer this question.

Acknowledgments

We thank Viola, O. P. Mahaney, C. Mahaney and G. Mahaney, Ajith Kumar, Suresh, Gail Coelho, Joan Voros, Merry Zacharias, Uma Fernandez, Gabriel Mahatma, Siva Prasad and Laurence Gaume for helping us in so many ways. This paper was written when R.K. had financial assistance from Chicago Zoological Society, International Primatological Society, Primate Conservation, Inc., Wildlife Conservation Society and National Geographic Society for studying the lion-tailed macaques. W.C.M.'s geophagy research is funded by York University and Quaternary Surveys (Toronto). We are indebted to Drs Frank E. Poirier, Jörg U. Ganzhorn, Inoue-Murayama, Tim Clutton-Brock, Deborah J. Overdorff and Deborah J. Curtis for answering a questionnaire on primate geophagy. Finally we thank the three anonymous referees for the constructive criticism.

References

- Altmann, S. A., Post, D. G. & Klein, D. F. 1987. Nutrients and toxins of plants in Amboseli, Kenya. *African Journal of Ecology*, **25**, 279–293.
- Arthur, W. J. & Alldredge, A. W. 1979. Soil ingestion by mule deer in North-Central Colorado. *Journal of Range Management*, **32**, 62–71.
- Aufreiter, S., Hancock, R. G. V., Mahaney, W. C., Stambolic-Robb, A. & Sanmugadas, K. 1997. Geochemistry and mineralogy of soils eaten by humans. *International Journal of Food Sciences and Nutrition*, **48**, 293–305.
- Bate-Smith, E. C. 1972. Attractants and repellents in higher animals. In: *Phytochemical Ecology* (Ed. by J. B. Harborne), pp. 45–56. London: Academic Press.
- Bennett, E. L. 1983. The banded langur: the ecology of a colobine in a West Malaysian forest. Ph.D. thesis, University of Cambridge.
- Bicca-Marques, J. C. & Calegario-Marques, C. 1994. A case of geophagy in the black howling monkey *Alouatta caraya*. *Neotropical Primates*, **2**, 7–9.
- Bolton, K. A., Campbell, V. M. & Burton, F. D. 1998. Chemical analysis of soils of Kowloon (Hong Kong) eaten by hybrid macaques. *Journal of Chemical Ecology*, **24**, 195–205.
- Caius, J. F. & Chhappgar, S. K. 1933. Earth-eating and salt-licking in India. *Journal of the Bombay Natural History Society*, **37**, 455–459.

- Cant, J. G. H. 1990. Feeding ecology of spider monkeys (*Ateles geoffroyi*) at Tikal, Guatemala. *Human Evolution*, **5**, 269–281.
- Clutton-Brock, T. H. 1972. Feeding and ranging behaviour of the red colobus monkey. Ph.D. thesis, University of Cambridge.
- Cooney, D. O. & Struhsaker, T. T. 1997. Adsorptive capacity of charcoals eaten by Zanzibar red colobus monkeys: implications for reducing dietary toxins. *International Journal of Primatology*, **18**, 235–246.
- Curtis, D. J. & Zaramody, A. 1998. Behaviour and ecology of the mongoose lemur. *Lemur News*, **3**, 20–21.
- Danford, D. E. 1982. Pica and nutrition. *Annual Review of Nutrition*, **2**, 303–322.
- Davies, A. G. & Baillie, I. C. 1988. Soil-eating by red leaf monkeys (*Presbytis rubicunda*) in Sabah, Northern Borneo. *Biotropica*, **20**, 252–258.
- Daykin, P. W. 1960. *Veterinary Applied Pharmacology and Therapeutics*. London: Baillière, Tindall & Cox.
- Diamond, J., Bishop, K. D. & Gilardi, J. D. 1999. Geophagy in New Guinea birds. *Ibis*, **141**, 181–193.
- Dittus, W. P. J. 1985. The influence of cyclones on the dry evergreen forest of Sri Lanka. *Biotropica*, **17**, 1–14.
- Eisenberg, J. F., Muckenhirn, N. A. & Rudran, R. 1972. The relation between ecology and social structure in primates. *Science*, **176**, 863–874.
- Eudey, A. A. 1978. Earth-eating by macaques in Western Thailand: a preliminary analysis. In: *Recent Advances in Primatology, Vol 1: Behavior* (Ed. by D. J. Chivers & J. Herbert), pp. 343–345. New York: Academic Press.
- Feeny, P. P. 1969. Inhibitory effect of oak leaf tannins on the hydrolysis of proteins by trypsin. *Phytochemistry*, **8**, 2119–2126.
- Fossey, D. 1983. *Gorillas in the Mist*. Boston: Houghton Mifflin.
- Fossey, D. & Harcourt, A. H. 1977. Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*). In: *Primate Ecology: Studies of Feeding and Ranging Behaviour in Prosimians, Monkeys and Apes* (Ed. by T. H. Clutton-Brock), pp. 415–447. London: Academic Press.
- Freeland, W. J. & Janzen, D. J. 1974. Strategies of herbivory in mammals: the role of plant secondary compounds. *American Naturalist*, **108**, 269–289.
- Ganzhorn, J. 1987. Soil consumption of two groups of semi-free-ranging lemurs (*Lemur catta* and *Lemur fulvus*). *Ethology*, **74**, 146–154.
- Glander, K. E. 1982. The impact of plant secondary compounds on primate feeding behaviour. *Yearbook of Physical Anthropology*, **25**, 1–18.
- Glander, K. E. 1994. Non-human primate self medication with wild plant foods. In: *Eating on the Wild Side* (Ed. by N. Etkin), pp. 227–239. Tucson: University of Arizona Press.
- Galtenboth, R. 1976. Non-human primates (apes, monkeys and prosimians). In: *Handbook of Zoo Medicine* (Ed. by H. G. Kloss & E. M. Lang), pp. 46–85. New York: Van Nostrand Reinhold.
- Goodall, J. 1965. Chimpanzees of the Gombe Stream Reserve. In: *Primate Behavior: Field Studies of Monkeys and Apes* (Ed. by I. DeVore), pp. 425–473. New York: Holt, Rinehart & Winston.
- Gurian, E., O'Neil, P. L. & Price, C. S. 1992. Geophagy and its relation to tannin ingestion in Rhesus macaques (*Macaca mulatta*). *AAZPA Regional Proceedings*, **1992**, 152–159.
- Hall, K. R. L. 1962. Numerical data, maintenance activities and locomotion in the wild chacma baboon, *Papio ursinus*. *Proceedings of the Zoological Society of London*, **139**, 181–220.
- Halstead, J. A. 1968. Geophagia in man: its nature and nutritional effects. *American Journal of Clinical Nutrition*, **21**, 1384–1393.
- Hemingway, C. A. 1998. Selectivity and variability in the diet of Milne-Edward's sifakas (*Propithecus diadema edwardsi*): implications for folivory and seed-eating. *International Journal of Primatology*, **19**, 355–377.
- Hesse, P. P. 1955. A chemical and physical study of the soils of termite mounds in East Africa. *Journal of Ecology*, **43**, 449–461.
- Heymann, E. W. & Hartmann, G. 1991. Geophagy in moustached tamarins, *Saguinas mystax* (Platyrrhini: Callitrichidae), at the Rio Blanco, Peruvian Amazonia. *Primates*, **32**, 533–537.
- Hirabuki, Y. & Izawa, K. 1990. Chemical properties of soils eaten by wild red howler monkeys (*Alouatta seniculus*): a preliminary study. *Field Studies of New World Monkeys, La Mascarena, Columbia*, **3**, 25–28.
- Hladik, C. M. 1977a. 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* (Ed. by T. H. Clutton-Brock), pp. 324–353. London: Academic Press.
- Hladik, C. M. 1977b. Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on diet. In: *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (Ed. by T. H. Clutton-Brock), pp. 481–501. London: Academic Press.
- Hladik, C. M. & Gueguen, L. 1974. Géophagie et nutrition minérale chez les primates sauvages. *Comptes Rendus des Séances de l'Académie des Sciences, Série D*, **279**, 1393–1396.
- Huffman, M. A. & Seifu, M. 1989. Observations on the illness and consumption of a possibly medicinal plant *Vernonia amygdalina* (Del.), by a wild chimpanzee in the Mahale Mountains National Park, Tanzania. *Primates*, **30**, 51–63.
- Hunter, J. & de Kleine, R. 1984. Geophagy in Central America. *Geographical Review*, **74**, 157–169.
- Inoue, M. 1987. Soil eating of Japanese macaques (*Macaca fuscata*) at Arashiyama, Kyoto. *Primate Research*, **3**, 103–111.
- Izawa, K. 1993. Soil eating by *Alouatta* and *Ateles*. *International Journal of Primatology*, **14**, 229–242.
- Izawa, K., Kimura, K. & Samper-Nieto, A. 1979. Grouping of the wild spider monkeys. *Primates*, **20**, 503–512.
- Janson, C. H. 1988. Intra-specific food competition and primate food structure: a synthesis. *Behaviour*, **105**, 1–17.
- Janzen, D. H. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica*, **6**, 69–103.
- Janzen, D. H. 1975. *The Ecology of Plants in the Tropics*. London: Edward Arnold.
- Johns, T. 1990. *With Bitter Herbs They Shall Eat it: Chemical Ecology and the Origins of Human Diet and Medicine*. Tucson: University of Arizona Press.
- Johns, T. & Duquette, M. 1991. Detoxification and mineral supplementation as functions of geophagy. *American Journal of Clinical Nutrition*, **53**, 448–456.
- Jones, L. M. 1957. *Veterinary Pharmacology and Therapeutics*. 2nd edn. Ames: Iowa State College Press.
- Julliot, C. & Sabatier, D. 1993. Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. *International Journal of Primatology*, **14**, 527–550.
- Ketch, C. 1998. Microbiological investigations of geophagy in chimpanzees. M.Sc. thesis, University of Toronto.
- Kinzey, W. G. & Norconk, M. A. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *International Journal of Primatology*, **14**, 207–227.
- Klaus, G., Klaus-Hügi, C. & Schmid, B. 1998. Geophagy by large mammals at natural licks in the rain forest of the Dzanga National Park, Central African Republic. *Journal of Tropical Ecology*, **14**, 829–839.
- Knezevich, M. 1998. Geophagy as therapeutic mediator of endoparasitism in a free-ranging group of rhesus macaques (*Macaca mulatta*). *American Journal of Primatology*, **44**, 71–82.
- Koshimizu, K., Ohigashi, H., Huffman, M. A., Nishida, T. & Takasaki, H. 1993. Physiological activities and the active

- constituents of potentially medicinal plants used by wild chimpanzees of the Mahale Mountains, Tanzania. *International Journal of Primatology*, **14**, 345–356.
- Kreulen, D. A.** 1985. Lick use by large herbivores: a review of benefits and banes of soil consumption. *Mammal Review*, **15**, 107–123.
- Kreulen, D. A. & Jager, T.** 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* (Ed. by F. M. C. Gilchrist & R. I. Mackie), pp. 204–221. Johannesburg: Science Press.
- Krishnamani, R.** 1994. Diet composition of the bonnet macaque (*Macaca radiata*) in a tropical dry evergreen forest of southern India. *Tropical Biodiversity*, **2**, 285–302.
- Laufer, B.** 1930. Geophagy. *Field Museum Natural History, Anthropological Service*, **18**, 97–198.
- Lindburg, D. G.** 1977. Feeding behaviour and diet of rhesus monkeys (*Macaca mulatta*) in a Siwalik forest in North India. In: *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (Ed. by T. H. Clutton-Brock), pp. 223–249. London: Academic Press.
- McKey, D. B.** 1978. Soils, vegetation and seed-eating by black colobus monkeys. In: *The Ecology of Arboreal Folivores* (Ed. by G. G. Montgomery), pp. 423–437. Washington: Smithsonian Institution Press.
- McKey, D. B., Gartlan, J. S., Waterman, P. G. & Choo, G. M.** 1981. Food selection by black colobus monkeys (*Colobus satanus*) in relation to plant chemistry. *Biological Journal of the Linnean Society*, **16**, 115–146.
- Mahaney, W. C.** 1987. Behaviour of the African buffalo on Mount Kenya. *African Journal of Ecology*, **25**, 199–202.
- Mahaney, W. C.** 1990. *Ice on the Equator*. Sister Bay, Wisconsin: Wm Caxton.
- Mahaney, W. C.** 1993. Scanning electron microscopy of earth mined and eaten by mountain gorillas in the Virunga mountains, Rwanda. *Primates*, **34**, 311–319.
- Mahaney, W. C. & Hancock, R. G. V.** 1990. Geochemical analysis of African buffalo geophagic sites and dung on Mount Kenya, East Africa. *Mammalia*, **54**, 25–32.
- Mahaney, W. C., Watts, D. P. & Hancock, R. G. V.** 1990. Geophagia by mountain gorillas (*Gorilla gorilla beringei*) in the Virunga mountains, Rwanda. *Primates*, **31**, 113–120.
- Mahaney, W. C., Hancock, R. G. V. & Inoue, M.** 1993. Geochemistry and clay mineralogy of soils eaten by Japanese macaques. *Primates*, **34**, 85–91.
- Mahaney, W. C., Aufreiter, S. & Hancock, R. G. V.** 1995a. Mountain gorilla geophagy: a possible seasonal behaviour for dealing with the effects of dietary changes. *International Journal of Primatology*, **16**, 475–488.
- Mahaney, W. C., Stambolic-Robb, A., Knezevich, M., Hancock, R. G. V., Aufreiter, S., Sanmugadas, K., Kessler, M. J. & Grynps, M. D.** 1995b. Geophagy amongst rhesus macaques on Cayo Santiago, Puerto Rico. *Primates*, **36**, 323–333.
- Mahaney, W. C., Bezada, M., Hancock, R. G. V., Aufreiter, S. & Perez, F. L.** 1996a. Geophagy of Holstein hybrid cattle in the Northern Andes, Venezuela. *Mountain Research and Development*, **16**, 177–180.
- Mahaney, W. C., Hancock, R. G. V., Aufreiter, S. & Huffman, M. A.** 1996b. Geochemistry and clay mineralogy of termite mound soil and the role of geophagy in chimpanzees of the Mahale Mountains, Tanzania. *Primates*, **37**, 121–134.
- Mahaney, W. C., Milner, M. W., Sanmugadas, K., Hancock, R. G. V., Aufreiter, S., Wrangham, R. W. & Pier, H. W.** 1997. Analysis of geophagy soils in Kibale Forest, Uganda. *Primates*, **38**, 159–175.
- Mahaney, W. C., Zippin, J., Hancock, R. G. V., Aufreiter, S., Campbell, S., Malloch, D., Wink, M. & Huffman, M. A.** In press. The geochemistry, mineralogy and biology of termite mound soils eaten by chimpanzees of the Mahale mountains in Tanzania. *Journal of Tropical Ecology*.
- Malik, I. & Southwick, C. H.** 1987. Feeding behaviour of free-ranging rhesus of Tughlaqabad. *Journal of the Bombay Natural History Society*, **84**, 336–349.
- Martin, R. D.** 1990. *Primate Origins and Evolution: A Phylogenetic Reconstruction*. Princeton, New Jersey: Princeton University Press.
- Matthews, B.** 1954. A discussion of the physiology of man at high altitude. *Proceedings of the Royal Society of London, Series B*, **143**, 1–4.
- Milton, K.** 1980. *The Foraging Strategy of Howler Monkeys*. New York: Columbia University Press.
- Milton, K.** 1984. The role of food-processing factors in primate food choice. In: *Adaptations for Foraging in Non-human Primates* (Ed. by P. S. Rodman & J. G. H. Cant), pp. 249–279. New York: Columbia University Press.
- Mloszewski, M. J.** 1983. *The Behaviour and Ecology of the African Buffalo*. Cambridge: Cambridge University Press.
- Moe, S. R.** 1993. Mineral content and wildlife use of soil licks in southwestern Nepal. *Canadian Journal of Zoology*, **71**, 933–936.
- Müller, K.-H., Ahl, C. & Hartmann, G.** 1997. Geophagy in masked titi monkeys (*Callicebus personatus melanochir*) in Brazil. *Primates*, **38**, 69–77.
- Newton, P.** 1992. Feeding and ranging patterns of forest hanuman langurs (*Presbytis entellus*). *International Journal of Primatology*, **13**, 245–285.
- Nishihara, T. & Kuroda, S.** 1991. Soil scratching behaviour by western lowland gorillas. *Folia Primatologica*, **57**, 48–51.
- Nishihara, T. & Uehara, S.** 1993. Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term records from Mahale Mountains, Tanzania. *African Study Monographs*, **3**, 109–130.
- Norris, J.** 1988. Diet and feeding behaviour of semi-free ranging mandrills in an enclosed Gabonais forest. *Primates*, **29**, 449–463.
- Oates, J. F.** 1977. The guereza and its food. In: *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (Ed. by T. H. Clutton-Brock), pp. 275–321. London: Academic Press.
- Oates, J. F.** 1978. Water-plant and soil consumption by guereza monkeys (*Colobus guereza*): a relationship with minerals and toxins in the diet? *Biotropica*, **10**, 241–253.
- Overdorff, D. J.** 1993. Similarities, differences, and seasonal patterns in the diets of *Eulemur fulvus rufus* and *Eulemur rubriventer* in the Ranomafana National Park, Madagascar. *International Journal of Primatology*, **14**, 721–753.
- Oyama, M. & Takehara, H.** 1970. *Standard Soil Color Charts*. Tokyo: Japan Research Council of Agriculture, Forestry and Fisheries.
- Petal, M. M.** 1978. The role of ants in ecosystems. In: *Production Ecology of Ants and Termites* (Ed. by M. V. Brain), pp. 293–307. Cambridge: Cambridge University Press.
- Poirier, F. E.** 1970. The Nilgiri langur (*Presbytis johnii*) of South India. In: *Primate Behaviour* (Ed. by L. A. Rosenblum), pp. 251–383. New York: Academic Press.
- Pollock, J. I.** 1975. Social behaviour and ecology of *Indri indri*. Ph.D. thesis. University of London.
- Pomeroy, D. E.** 1983. Some effects of mound-building termites on the soils in a semi-arid area of Kenya. *Journal of Soil Science*, **34**, 555–570.
- Rhoades, D. F. & Cates, R. G.** 1976. Toward a general theory of plant antiherbivore chemistry. In: *Recent Advances in Phytochemistry, Vol. 10. Biochemical Interaction Between Plants and Insects* (Ed. by J. W. Wallace & R. Mansell), pp. 168–213. New York: Plenum.
- Richards, P. W.** 1975. *The Tropical Rainforest: an Ecological Study*. 5th reprint. Cambridge: Cambridge University Press.
- Ripley, S.** 1970. Leaves and leaf-monkeys: the social organisation of foraging in grey langurs *Presbytis entellus thersites*. In: *Old World*

- Monkeys: Evolution, Systematics and Behaviour* (Ed. by J. R. Napier & P. H. Napier), pp. 481–509. New York: Academic Press.
- Robbins, C. T.** 1983. *Wildlife Feeding and Nutrition*. New York: Academic Press.
- Rogers, M. E., Maisels, F., Williamson, E. A., Fernandez, M. & Tutin, C. E. G.** 1990. Gorilla diet in the Lopé Reserve, Gabon: a nutritional analysis. *Oecologia*, **84**, 326–339.
- Rowe, N.** 1996. *The Pictorial Guide to the Living Primates*. New York: Pogonios Press.
- Ruggiero, R. G. & Fay, J. M.** 1994. Utilization of termitarium soils by elephants and its ecological implications. *African Journal of Ecology*, **32**, 222–232.
- Salick, J., Herrera, P. & Jordan, C. F.** 1983. Termitaria: patchiness in nutrient-deficient rain forests. *Biotropica*, **15**, 1–7.
- Schaller, G. B.** 1963. *The Mountain Gorilla: Ecology and Behavior*. Chicago: University of Chicago Press.
- Schaller, G. B.** 1965. The behaviour of the mountain gorilla. In: *Primate Behavior: Field Studies of Monkeys and Apes* (Ed. by I. DeVore), pp. 324–367. New York: Holt, Rinehart & Winston.
- Setz, E. Z. F. & Enzweiler, J.** 1992. Geophagy by golden faced sakis (*Pithecia pithecia chrysocephala*) in central Amazon. *Proceedings of the XIVth Congress of the International Primatological Society, Strasbourg*, **319** (abstract).
- Sinclair, A. R. E.** 1977. *The African Buffalo: A Study of Resource Limitation of Populations*. Chicago: University of Chicago Press.
- Stambolic-Robb, A.** 1997. Geophagy amongst free-ranging Sumatran orang-utans (*Pongo pygmaeus abelii*) of Gunung Leuser National Park and ex-captive orang-utans (*Pongo pygmaeus pygmaeus*) of Sungai rain forest, Indonesia. M.Sc. thesis, York University.
- Stanford, C. B.** 1991. The capped langur in Bangladesh: behavioural ecology and reproductive tactics. *Contributions to Primatology*, **26**, 1–179.
- Stickney, J. C. & van Liere, E. J.** 1953. Acclimatization to low oxygen tension. *Physiological Review*, **33**, 13–34.
- Struhsaker, T. T.** 1975. *The Red Colobus Monkey*. Chicago: University of Chicago Press.
- Struhsaker, T. T., Cooney, D. O. & Siex, K. S.** 1997. Charcoal consumption by Zanzibar red colobus monkeys: its function and its ecological and demographic consequences. *International Journal of Primatology*, **18**, 61–72.
- Swain, T.** 1979. Tannins and lipids. In: *Herbivores: Their Interactions with Secondary Plant Metabolites* (Ed. by G. A. Rosenthal & D. H. Janzen), pp. 657–682. New York: Academic Press.
- Uehara, S.** 1982. Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudacanthotermes spiniger*). *Folia Primatologica*, **37**, 44–76.
- Underwood, E. J.** 1977. *Trace elements in Human and Animal Nutrition*. New York: Academic Press.
- Von dem Bussche, G. H. & Van der Zee, D.** 1985. Damage by samango monkeys to pine trees in the Northern Transvaal. *South African Forestry Journal*, **133**, 43–48.
- Vermeer, D. E. & Ferrell, R. E. Jr** 1985. Nigerian geophagial clay: a traditional anti-diarrhoeal pharmaceutical. *Science*, **227**, 634–636.
- Walkley, A. & Black, I. A.** 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Science*, **37**, 29–38.
- Watts, D. P.** 1984. Composition and variability of mountain gorilla diets in the central Virungas. *American Journal of Primatology*, **7**, 323–356.
- Weir, J. S.** 1969. Spatial distribution of elephants in an African National Park in relation to environmental sodium. *Oikos*, **23**, 1–13.
- Weir, J. S.** 1973. Air flow, evaporation and mineral accumulation in mounds of *Macrotermes subhyalinus* (Rambur). *Journal of Animal Ecology*, **42**, 509–520.
- Wheatley, B. P.** 1980. Feeding and ranging of east Bornean *Macaca fascicularis*. In: *The Macaques: Studies in Ecology, Behavior and Evolution* (Ed. by D. G. Lindburg), pp. 215–246. New York: Van Nostrand Reinhold.
- White, F. J.** 1989. Diet, ranging behaviour and social organization of the black and white ruffed lemur, *Varecia variegata variegata*, in southeastern Madagascar. *American Journal of Physical Anthropology*, **78**, 323 (abstract).
- Wiley, A. S. & Katz, S. H.** 1998. Geophagy in pregnancy: a test of a hypothesis. *Current Anthropology*, **39**, 532–545.
- Williamson, E. A., Tutin, C. E. G., Rogers, M. E. & Fernandez, M.** 1990. Composition of the diet of lowland gorillas at Lopé in Gabon. *American Journal of Primatology*, **21**, 265–277.
- Wood, T. G. & Sands, W. A.** 1978. The role of termites in ecosystems. In: *Production Ecology of Ants and Termites* (Ed. by M. V. Brain), pp. 55–80. Cambridge: Cambridge University Press.
- Wrangham, R. W.** 1977. Feeding behaviour of chimpanzees in Gombe Stream National Park. In: *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (Ed. by T. H. Clutton-Brock), pp. 503–538. London: Academic Press.
- Wrangham, R. W. & Goodall, J.** 1989. Chimpanzee use of medicinal leaves. In: *Understanding Chimpanzees* (Ed. by P. G. Heltne & L. A. Marquardt), pp. 22–37. Cambridge, Massachusetts: Harvard University Press.
- Wrangham, R. W. & Nishida, T.** 1983. *Aspilia* spp. leaves: a puzzle in the feeding behaviour of wild chimpanzees. *Primates*, **24**, 276–282.
- Zhao, Q., Deng, Z. & Xu, J.** 1991. Natural foods and their ecological implications for *Macaca thibetana* at Mount Emei, China. *Folia Primatologica*, **57**, 1–15.
- Zippin, J.** 1998. Geophagy amongst chimpanzees of Mahale Mountains National Park, Tanzania. M.Sc. thesis, York University.

Appendix

Physical characteristics

Soils consumed by primates are usually reddish to reddish brown in colour (see the Soil Color Charts of [Oyama & Takehara 1970](#) as a guide to the colour chips). The documented 2.5–7.5 YR (YR=yellow red) colours indicate that comestible soils have a long weathering history with depleted silica as a result of strong leaching and liberated oxides often high in iron ([Mahaney et al. 1995a, 1996b, 1997](#)). The yellow colours often indicate released hydroxides of iron or aluminium and signify high clay content.

Research on consumed natural earth shows a preponderance of clay size material with minimum quantities of silt and sand ([Mahaney 1990, 1993; Mahaney et al. 1990, 1993, 1996a, b, 1997](#)). It would be wise to show these distributions on probability diagrams with a curve that indicates the exact proportion of individual sand, silt and clay fractions. For example, there may be 30% silt in a sample, but it would be useful to know if this is fine or coarse silt. While considering fine silt fractions or fractions of less than 16 µm, it would be even more useful and important to know how much was in the 8–4- or 8–2-µm grade sizes. Similarly in the 8–2-µm fractions, some of the silt might act like clay and be capable of adsorbing toxins and plant metabolites.

Clay content is generally reported without any accompanying information on clay mineral composition even though it is possible to have 10 or even 20% clay without

any clay minerals present in the sample. Although clay size is important, clay mineral distribution and knowledge of individual clay species is essential to say anything about the toxin adsorption capacity of the clay.

Adherence of small particles in consumed soil is rarely studied despite their importance and their distinction from control or refused (uneaten) soils. Since geophagy is a tropical phenomenon, soils are so well leached that 2:1 (Si: Al=2:1) clay minerals are mostly eradicated, making it difficult to form soil structures that rely on adherence of sticky or expandable clay. Soil structures ranging from platy to blocky, granular, prismatic and columnar are often related to the percentage of clay size mineral. This aspect as a stimulus for geophagy needs further investigation.

Mineralogy

The mineralogy of consumed earth includes primary and secondary minerals. The former can be looked at in terms of the analysis of groups by size, from sand to clay, and the latter on the basis of density from ultra heavy to light. Since these analyses require considerable time, a study of specific suites of samples is more likely to yield significant results.

Previous studies have provided insufficient information on the local bedrock, presence or absence of transported materials overlying the bedrock and their different lithology, and relationship of the regolith (all unconsolidated material overlying bedrock) to the soil being consumed on a regular or irregular basis by primates. This longitudinal cross-section reveals not only the comestible material, but also the samples refused. A comparative analysis of the eaten and uneaten samples will show the benefits of consuming a particular material.

As a practical first approximation it is easiest and most instructive to draw off the residual after particle size analysis, equilibrate the slurry in a shaker, and then centrifuge a subsample on to ceramic tiles and allow it to air dry. Once air dried it can be analysed by X-ray diffraction. Subsequently, the key clay and primary minerals can be traced and identified and their relative amounts established (see for example [Aufreiter et al. 1997](#); [Mahaney et al. 1997](#)). Later they can be glycolated at 65°C and analysed to establish the presence or absence of expandable clay minerals. This is normally followed by traces at 300, 500 and 550°C to establish the dehydration characteristics known to accompany certain clay species. This gives powerful data related to the composition of the <2-µm fraction where the colloidal material might be available to adsorb toxins of various kinds.

After X-ray diffraction, the sand fraction can be analysed by scanning electron microscope (SEM) and energy dispersive spectrometry (EDS) to observe the degree of etching and dissolution that has occurred on the sands consumed. This will quickly confirm the weathered state of the eaten material and most importantly it will provide information on sand coatings and their composition. Since coatings are often Fe- or Mn-rich their importance as macro- or microelements and their possible availability to animals eating them can be established. The degree to which SEM-EDS analysis is carried

out depends on the problem and the availability of funds, but it is expensive. However, the results are of unparalleled significance (see [Mahaney et al. 1996b, 1997](#)).

High-resolution multispectral analysis is possible after gravimetric separation of the ultraheavy through light sands and silts in a sample ([Mahaney et al. 1997](#)). Here one has the possibility of separating the light minerals (quartz and feldspar) through the light heavy (hornblende, mica) to heavy (magnetite, ilmenite) and ultraheavy (gold) to determine the degree to which even resistant minerals such as rutile and zircon have been affected by weathering.

While not directly beneficial to the animal eating them, rutile and zircon indicate dissolution, similar to the light minerals of which the feldspars are the most prevalent. Both have relative rates at which they can slowly release ions into the soil to be consumed by various species. Some ions, such as calcium, might be beneficial; others, such as thorium, that are radioactive might have adverse effects if they become trapped in the tissue or lodged in the intestine. Heavy minerals containing sulphur (pyrite for example) might have beneficial effects even when consumed in minute amounts. What is most useful is a complete spectral analysis of the minerals present and their degree of dissolution; for example, fresh to weathered state.

Chemistry

Previous geophagy research (e.g. [Davies & Baillie 1988](#)) has relied on superficial chemical analyses of selected chemical elements such as the common alkali metals and alkaline earths, sometimes with or without cation exchange capacity and pH. This could be considered a bare minimum of what is required and one has to be very careful about drawing conclusions from such a limited database. To be sure pH trends establish acidity to alkalinity between consumed and control soils, it might be useful to look at acidosis and antacid treatment, as a starting point.

In addition to pH, calcium, sodium, magnesium and Ca cations and cation exchange capacity (CEC), it is essential to know the total concentrations of carbon, nitrogen and hydrogen, preferably from a carbon-hydrogen-nitrogen (CHN) analyser. The organic carbon, if different from the total carbon, should be determined by the Walkley & Black method to determine precise differences between eaten and consumed samples ([Walkley & Black 1934](#)). From the basic cations and the CEC, base saturation needs to be determined to approximate the leaching intensity of the soils. Every effort should be made to relate colour to the soil chemistry, especially the concentration and distribution of organic matter.

To obtain information on the concentrations of elements that are not obtainable through routine geochemical analyses, it is often necessary to use atomic absorption spectrophotometry. These elements include selenium, phosphorus and silicon. Selenium is necessary for muscle strength, phosphorus for various physiological requirements and silicon may be important for

connective tissue regeneration. Silicon (as SiO_2) also indicates the leaching history of the soil.

Geochemistry

Instrumental neutron activation analysis (INAA) provides the most economical means of deriving data on the concentrations of macroelements, microelements and trace elements in a sample, apart from conducting mass spectrometry on subsamples of the material collected. With INAA one has access to a matrix of 34 chemical elements, from low to high atomic number, that provides information on the concentrations present. The macroelements such as calcium, magnesium, sodium, potassium, aluminium, iron and titanium are available to provide background data on the lithic material, as well as the retention of insoluble material such as iron and the removal of soluble material such as calcium and sodium. The relative elemental ratios in the consumed soil, when tested against the parent material from which the soil formed, provide valuable information on the age of the soil as well as the reservoir of elements important in nutrition and diet and possibly zoopharmacognosy.

Within the realm of the microelements (manganese, barium, chlorine, strontium, cerium) only manganese and chlorine are of likely importance in geophagy. Chlorine, almost at detection limits, has never been shown to be in the form of sodium chloride as a stimulus for geophagy behaviour (Mahaney et al. 1997). Manganese, while important along with iron in many geophagy studies (Mahaney et al. 1997), is often overlooked. Cerium, which is an important rare earth element, although not a direct stimulus in geophagy, indicates the presence of phosphates which may play an important role in geophagy. The likely trace elements including arsenic, bromine, cobalt, chromium, copper, iodine and antimony are all detected by INAA and have variable importance in geophagy. The rare earth elements (REEs), while not known to have importance in geophagy, are very important in establishing the uniformity of the ingested material versus the control soils (Mahaney et al. 1997). The resulting geochemical profile, showing the light and heavy REEs, establishes their variation and allows determination of the geochemical homogeneity of the ingested material.