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ORIGINAL ARTICLE

Observations of termitarium geophagy by Rylands' bald-faced saki monkeys (*Pithecia rylandsi*) in Madre de Dios, Peru

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Abstract Geophagy, or soil consumption, has been documented in diverse animal taxa, including many primates. Physiological functions such as mineral supplementation, detoxification of secondary compounds, and antacid properties are possible causes for this behavior. We report on observations of geophagy at arboreal termitaria by free-ranging *Pithecia rylandsi* at La Estación Biológica Los Amigos (EBLA) in Perú between 2008 and 2015. Characteristics of geophagy events, including saki monkey behavior at the termitaria, were recorded and geochemical analyses were conducted on consumed termitaria, nearby topsoils, and unvisited termitaria. We observed 76 feeding bouts at 26 different termitaria by two groups of *P. rylandsi* during 1125 observational hours (0.07 bouts/obs. h). Geophagy occurred throughout the year, but rates peaked in January during the rainy season. All age and sex classes visited both active and inactive mounds. Feeding bouts were brief (171 ± SD 154 s), and no differences were observed in time spent feeding at active or inactive termitaria. Analyses showed that consumed soils contained higher concentrations of phosphorous, potassium, calcium, and magnesium than did topsoil. Consumed soils also contained a higher total cation exchange capacity than topsoil. Our analysis of consumed versus control termitaria revealed no differences in their chemical composition. We discuss these results in the context of the two primary hypotheses proposed for geophagy in pitheciins: mineral supplementation and toxin adsorption. Our data are consistent with the interpretation that *P. rylandsi* consume soils from arboreal termitaria to aid in adsorption of toxins found in immature seeds, which are a year-round component of their diet.

Keywords *Pithecia* · Geophagy · Soil composition · Feeding ecology · Nutritional supplementation · Tannin adsorption

Introduction

Geophagy, or consumption of soil-like materials, has been observed in diverse animal taxa including many primates (Krishnamani and Mahaney 2000). Several functions for geophagy have been proposed, including treatment of endoparasites, acid neutralization, prevention of diarrhea, mineral supplementation, and adsorption of toxins (Vermeer and Ferrell 1985; Davies and Baillie 1988; Müller et al. 1997; Knezevich 1998). These explanations are nonexclusive, as geophagy may serve multiple physiological functions that vary among as well as within taxa based on context (Krishnamani and Mahaney 2000).

Observations of geophagy have been reported for all major platyrrhine primate groups, but the behavior appears most commonly in atelids and pitheciids at South American Amazonian sites (Ferrari et al. 2008). In some species

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of callitrichids and cebids, geophagy is suggested to occur when soil matrix adhering to insects is ingested with them. However, as the soil consumption appears incidental, the soil itself may serve no distinct function for the primates. Among pitheciids, nearly all reported instances of soil consumption have been on termitaria (Ferrari et al. 2008). Based on the habitats and diets of these taxa, Ferrari et al. (2008) suggest that arboreal access to termitaria might be the primary reason for their predominance as soil sources.

Neotropical forests contain nutrient-poor soils due to leaching (Vitousek and Sanford 1986), but soils from termite mounds, which are composed of soil particles, organic matter, and nutrient-rich fecal material and salivary secretions (Noirot 1970), contain rich concentrations of certain minerals (Ferrari et al. 2008). In addition, termitaria may be finer-grained than the soils from which they are made, due to the mound construction process (Voros et al. 2001), and the soil can be manipulated as aggregated clumps, which facilitates handling (as suggested for *Callicebus* by Müller et al. 1997). Thus, termitaria may serve as localized and more accessible sources of minerals in nutrient-deficient environments (Krishnamani and Mahaney 2000). There is some evidence that this may be the case in pitheciids. For example, Setz et al. (1999) found that *Pithecia pithecia* fed on termitaria that contained higher levels of calcium (Ca), potassium (K), and magnesium (Mg) than did site topsoil, which suggests that termitaria are not only more easily accessed soils, but may have special properties for nutrition supplementation. Other minerals found in high quantities in termitaria include sodium (Na), iron (Fe), and phosphorous (P) (Holt and Lepage 2000).

While mineral supplementation may explain geophagy in some animals, those with diets composed mostly or entirely of plant parts may consume soils to address other challenges (Voight et al. 2008). Vegetation such as fruits, seeds, and young leaves that grow in nutrient-poor soils is often rich in toxic compounds like phenols and strychnine, which may have evolved as a chemical defense against predation by herbivores (Janzen 1974; Janzen et al. 1977). Geophagy may aid in countering the effects of these toxins, because properties found in some soils are known to buffer against tannins or have toxin-binding effects (Wakibara et al. 2001). For example, Amazonian parrots are reported to consume soils that contain higher clay content and cation exchange capacity (CEC), which are properties predicted to positively correlate with toxin adsorption (Gilardi et al. 1999). The ability for soils to bind or buffer toxins may be particularly important for pitheciins, which, like parrots, are habitual seed predators. While seeds consumed by sakis are shown to have overall higher nutritional content (i.e. high levels of lipids and proteins) than fruit pulp, they also contain moderate to high levels of condensed and bioactive tannins, thus posing a toxic risk (Kinzey and Norconk 1993; Norconk and Conklin-Brittain 2004).

Among pitheciids, geophagy has been reported for *P. pithecia* at sites in Venezuela and Brazil (Kinzey and Norconk 1993; Setz et al. 1999; Urbani et al. 2005), *P. monachus* in Bolivia (Izawa 1975), and *Callicebus torquatus* and *Chiropotes satanas* in Brazil (Müller et al. 1997; Veiga and Ferarri 2007). The results of these studies are largely ambiguous, but evidence most strongly points toward either mineral supplementation or toxin adsorption as primary drivers of geophagy.

Here, we describe the first observations of geophagy in a population of free-ranging saki monkeys, *Pithecia rylandsi*, at a field site in the Peruvian Amazon. We compare mineralogical, geochemical, and physical properties of consumed termitaria with control samples to evaluate the function of this behavior. We investigate the hypotheses that sakis consume soils either (1) for mineral supplementation or (2) as a digestive aid to mitigate effects of secondary compounds in their diet. If the monkeys consume soil from sources that are higher in concentrations of micronutrients, this would support a mineral supplementation function. If they consume soil from sources with higher clay content and CEC, this would support the function of geophagy in mitigating the effects of secondary compounds in their diet.

Methods

Study site and data collection

All observations were made at La Estación Biológica Los Amigos (EBLA) in the Department of Madre de Dios in southeastern Amazonian Peru, located at 12°34′07″S 70°05′57″ W. EBLA is a 453-ha research site located at the confluence of the Los Amigos and Madre de Dios Rivers, adjacent to the 146,000-ha Los Amigos Conservation Concession (Pitman 2010). EBLA was established in 2000 and hosts a diversity of vegetation types, including ‘upland’ terra firme forest with both primary and secondary successional components, bamboo stands, riparian forest, and aguajal swamp (Pitman 2010). Mean annual precipitation for 9 years with complete data for the site between 2001 and 2011 was 2584 mm, with a dry season from April through September (Atrium 2008; Palminteri et al. 2012; Watsa 2013).

Observations of geophagy by *P. rylandsi* were made during a long-term study on saki monkey behavior and ecology. Data were collected during periods of varying lengths in 2008 and from 2010 to 2015. Monkeys were already habituated to humans through the long-term presence of researchers at the site since 2000, as well as a previous multi-year study focusing on five saki monkey groups at EBLA (Palminteri et al. 2012). The saki population at EBLA was identified in the literature as *P. irrorata* prior to Marsh's (2014) taxonomic revision.

The current research focuses on two groups that inhabited home ranges of 33.2 ha (group A) and 47.5 ha (group B), with a 4.5-ha area of overlap between groups. Home ranges were calculated using GPS locations collected every 15 min during full-day follows in continuous sampling months from 2014 to 2015. We used minimum convex polygons (MCP) to determine home ranges, which is the method that has been most often applied across studies on sakis to date (Peres 1993; Vié et al. 2001; Boyle et al. 2009; Thompson 2011). Home ranges on this population of sakis from a previous long-term study were different from those reported here (see Palminteri and Peres 2012), which may be related to sampling effort, different estimation methods, or variation in the groups' ranging behavior over time. The research did not involve capturing or marking the animals. Individual saki monkey groups could be reliably identified based on their use of stable home ranges, group size and composition, and response to observers. Different age classes (infant, juvenile, adult) and adult males and females could be identified based on size differences. In all cases, ad libitum notes were taken to document feeding bouts, including location, time spent at termitaria, age/sex class of individuals feeding, how the soil was handled, and other feeding behavior. We inspected termitaria after feeding bouts to determine whether termites were present.

Soil samples were collected in 2012 for compositional analysis. Nine samples were collected from termitaria fed on by the sakis, representing all termitaria that were visited up to that point by the two principal study groups. Topsoil samples were also collected at the bases of two termitaria trees. Four control samples were collected from unvisited termitaria within the saki monkey group ranges; at two of these sites, samples were also collected from the associated topsoil. The control termitaria were selected based on similar gross appearance (e.g. relatively similar dimensions) and proximity to consumed termitaria, such that these mounds were bypassed by the sakis prior to feeding on consumed mounds. Due to time and budget constraints, we were unable to collect additional soil samples for analysis after 2012; however, we observed no significant differences in geophagy rates or behaviors prior to and after this year.

Soil and data analysis

The geochemical and physical properties analyzed (listed in Tables 3, 4) were chosen based on their association with physiological functions in other primates and granivorous vertebrates (Bolton et al. 1998; Setz et al. 1999; Krishnamani and Mahaney 2000; De Souza et al. 2002; Brightsmith et al. 2008). Soil analyses were performed by the Laboratorio de Análisis de Suelos at the Universidad Nacional Agraria La Molina in Lima, Peru. The pH of each sample was measured in a 1:1 soil-to-distilled water ratio. The CEC was obtained using the ammonium acetate (NH_4OA_c) method described in Tan (1996), and calculated in meq/100 g of soil.

Total mineral concentrations in the soil were determined by adding 1 g of powdered soil to a HCl solution at pH 2.0 and agitating the mixture for 1 h at 38 °C (Hunter and De Kleine 1984). The mix was centrifuged, and available concentrations of Ca, Mg, K, Na, and Fe were determined using atomic absorption spectrophotometry (see Gilardi et al. 1999; Brightsmith et al. 2008). Results were presented in parts per million. Available phosphorous was determined through extraction of 0.5 m sodium bicarbonate ($NaHCO_3$) at pH 8.5 (Olsen et al. 1954), with results also reported in parts per million. Finally, particle size distribution in soil samples was measured according to the procedure described by Brightsmith et al. (2008) and classified into three size categories based on percentage of dry weight: sand (>0.05 mm), silt (0.002–0.05 mm), and clay (<0.002 mm).

We used IBM SPSS 22.0 (SPSS, Chicago, IL) and R 3.1.2 (R Development Core Team 2015) software packages to analyze data. All statistical analyses were two-tailed, with significance set at $P < 0.05$. We used Mann–Whitney *U* tests to examine differences in time spent feeding on active and inactive termitaria, rates of geophagy in wet and dry seasons, and time spent feeding by age/sex classes. There were no significant behavioral differences between the study groups; thus a group-level comparison was not included in the analysis. We also used Mann–Whitney *U* tests to examine differences in soil characteristics between termitaria and topsoil samples. We conducted Spearman's rank correlation to test for a relationship between monthly rates of geophagy and rainfall. Lastly, soil characteristics of consumed and unconsumed termitaria were analyzed using Student's *t*-tests. We conducted stepwise Bonferroni corrections on soil characteristics to reduce the likelihood of type I errors. We did not conduct a habitat-level analysis on termitaria soil characteristics, because nearly all of the consumed termitaria (24 of 26) were located in upland terra firme forests.

Results

Field observations

We observed 76 feeding bouts at 26 different termitaria (Table 1) by two focal groups of *P. rylandsi* during 1125

Table 1 Characteristics of termitaria consumed by *P. rylandsi* at EBLA

Termitarium	Number of bouts[a]	Number of years visited	Group	Active/inactive[b]	Habitat type[c]	Total time feeding (s)[d]
1	8	3	A, B	I	TF	2410
2	6	3	B	I, A	TF	3647
3	3	3	B	A	TF	3715
4	15	4	A, B	A, I	TF	5189
5	1	1	B	I	TF	130
6	1	1	B	A	TF	72
7	1	1	B	I	TF	146
8	1	1	B	A	TF	64
9	1	1	B	I	TF	100
10	2	1	A	I, A	FP	260
11	1	1	B	A	TF	360
12	3	1	B	A	TF	610
13	10	2	A	A, I	TF	2625
14	6	2	B	A	TF	790
15	3	2	B	A, I	TF	1466
16	2	1	B	A	TF	203
17	1	1	B	A	TF	30
18	3	2	A	A	TF	525
19	1	1	A	A	TF	360
20	1	1	A	A	FP	60
21	1	1	B	I	TF	30
22	1	1	B	A	TF	120
23	1	1	B	I	TF	420
24	1	1	A	A	FP	120
25	1	1	B	I	TF	90
26	1	1	B	A	TF	120

[a] Number of geophagy bouts observed at each termitarium

[b] Indicates whether termitaria were active (A) or inactive (I) at time of consumption

[c] Habitat type denotes whether termitaria were located in terra firme (TF) or lowland floodplain (FP) forests

[d] Total feeding time is the total length of feeding in seconds for all individuals that fed at each mound

observation hours (0.07 bouts/obs. h). Observations are not equally distributed across months or years (Table 2); however, geophagy rates were consistent prior to and following 2014, when monthly observation hours were more balanced. We defined a feeding bout as a visit by a group of saki monkeys to a termitarium during which feeding occurred by one or more individuals. On two different days the same group visited the same termitarium within a 20-min period, and these sequential visits were considered a single bout. On the only other occasion on which the same monkey group revisited the same termitarium within a day, the visits were separated by nearly 7 h, and those visits were considered distinct bouts. In all instances, sakis consumed pieces from arboreal termitaria located at heights of 5-15 m. Termites were present in 66% of observed cases, indicating more active than inactive mounds consumed. Sakis were sometimes observed to consume termites with soil when feeding at active mounds, although it could not be reliably determined that all consumed pieces from these mounds contained termites. Three mounds (T-4, T-13, and T-15) appeared to change from active to inactive states between observed saki visits separated by intervals of 3, 2, and 5 months, respectively. Two other mounds (T-2 and T-10) that showed no termite activity appeared active during geophagy performed 15 and 30 months later. Soils from these mounds were consumed in both active and inactive conditions.

There were no differences in the amount of time spent feeding by individuals at active and inactive termitaria (Mann–Whitney U test: $Z = -0.681$, $P = 0.496$). To account for a potential sampling bias, we also examined differences in the amount of time spent feeding at active

Table 2 Observation hours on both saki groups during the study period

	2008	2010	2012	2013	2014	2015	Total
Jan						42.6	42.6
Feb						52.9	52.9
Mar						41.4	41.4
Apr						33.4	33.4
May	6.1					37.6	43.7
Jun	57.6		39.7	33.0	46.7	36.7	213.7
Jul	56.1		38.7		87.6	19.6	202.0
Aug	14.0	16.0			66.1		96.1
Sep					73.7		73.7
Oct					70.2		70.2
Nov		76.4			52.7		129.1
Dec		69.8			56.8		126.6
Total	133.8	162.2	78.4	33.0	453.8	264.2	1125.4

and inactive termitaria only during full-day follows (i.e. from sleep site to sleep site) from June 2014 to July 2015, when monthly observation hours were continuous; however, results remained insignificant (Mann–Whitney *U* test: $Z = -0.355$, $P = 0.723$). Two mounds, T-1 ($N = 8$ visits, total feeding time = 40.2 min) and T-4 ($N = 15$ visits, total feeding time = 105.5 min) are located in the small area of overlap between the two study groups and were utilized by both groups over a 3- to 4-year period. Visits stopped when the termitaria were gone, either through consumption by the sakis or other animals, or due to weathering and degradation. T-1 was inactive throughout the years it was used, while T-4 was active for all but the last few months of use.

Geophagy occurred in all months during which the sakis were observed, but rates peaked in the wet season month of January (Fig. 1). Our initial analysis revealed no significant trend in seasonal frequency of geophagy (Mann–Whitney *U* test: $Z = -1.200$, $P = 0.230$). However, when the analysis was limited to data collected during full-day follows in continuous sampling months from 2014 to 2015, geophagy rates were significantly higher in the wet season (Mann–Whitney *U* test: $Z = -2.526$, $P = 0.012$). Monthly rates of geophagy were positively correlated with rainfall during these continuous sampling months (Fig. 2).

The movement of one or several individuals directly to the mound usually initiated feeding events at termitaria. Sakis visited multiple mounds on nine observation days, and on some of these days they moved from one mound to the other without stopping to feed on fruits or other nearby food sources. Individuals typically utilized lianas draped around or near tree trunks as substrate supports while feeding. They accessed mounds simultaneously or by taking turns feeding while others rested on nearby supports. They typically removed parts of a mound by hand and at times visually inspected and manipulated pieces by breaking them further apart or licking them, although removed pieces were sometimes placed directly into the mouth without prior visual or manual inspection. They were occasionally observed licking or biting pieces directly from the mound (see supplementary material).

Total feeding time by all individuals at termitaria was 394 min. Feeding events, during which individual sakis handled and consumed soil, were typically brief, with a median of 120 s (range 10–1020 s). In 35 of the bouts (46%), only a single individual fed from a termitarium. We observed adults of both sexes and infants and juveniles (sex indeterminate) feeding from termitaria. Infants were observed to feed from termitaria in 5% of bouts in which an infant was present, while juveniles were observed to feed from termitaria in 49% of bouts, and adults were involved in 78% of bouts. There were no differences in the duration of geophagy among adult males, adult females, and juveniles (Mann–Whitney *U* test: adults vs. juveniles, $Z = -1.088$, $P = 0.276$; adult males vs. adult females, $Z = -0.298$, $P = 0.766$). This pattern of feeding duration among adult males, adult females, and juveniles remained insignificant when the analysis was limited to data collected during full-day follows from continuous sampling months between June 2014 and July 2015 (Mann–Whitney *U* test: adults vs. juveniles, $Z = -1.143$, $P = 0.253$; adult males vs. adult females, $Z = -0.386$, $P = 0.699$). Individuals of all age and sex classes were occasionally observed to scent-mark near termitaria. Agonistic interactions were observed at termitaria on rare occasions and were initiated by adults of both sexes and juveniles. These behaviors included chasing individuals away from the mound, displacements, pulling fur, and attempting to take termitarium pieces from others.

Soil geochemistry

Analyses of 13 soil samples from termitaria (9 visited and 4 unvisited/controls) in the saki groups' home ranges (Fig. 3) and four samples from topsoil at the base of trees below termitaria indicated some differences between termitaria and topsoil (Table 3). Termitarium samples were less acidic ($Z = -2.946$, $P = 0.003$) and had a higher CEC, an indicator of soil fertility, than topsoil samples ($Z = -2.549$, $P = 0.006$). Termitaria also contained a significantly higher percentage of organic carbon (C) ($Z = -2.158$, $P = 0.031$) and significantly higher concentrations of Ca, Mg, K, and P cations. There were no significant differences in Na and Fe concentrations. Analysis of particle size distribution revealed no significant

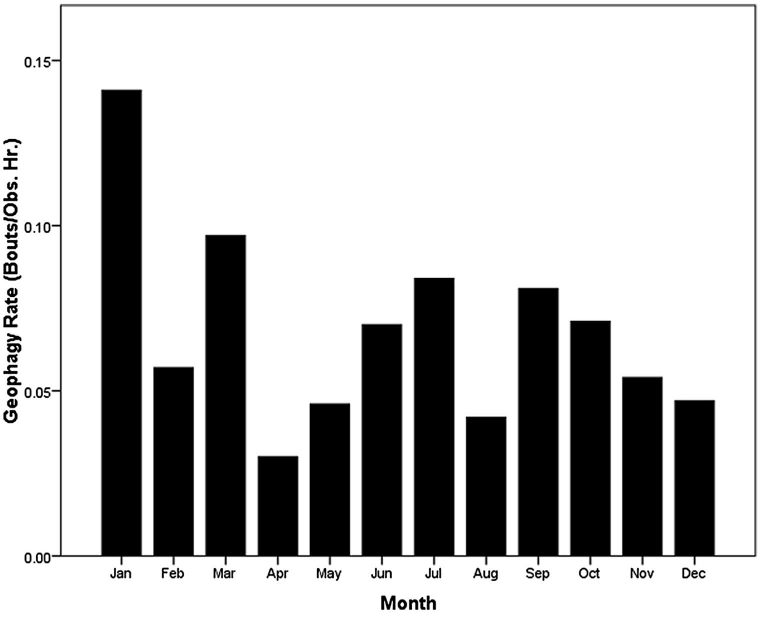

Fig. 1 Monthly rates of geophagy throughout the entire study period, measured as the number of bouts per observation hour

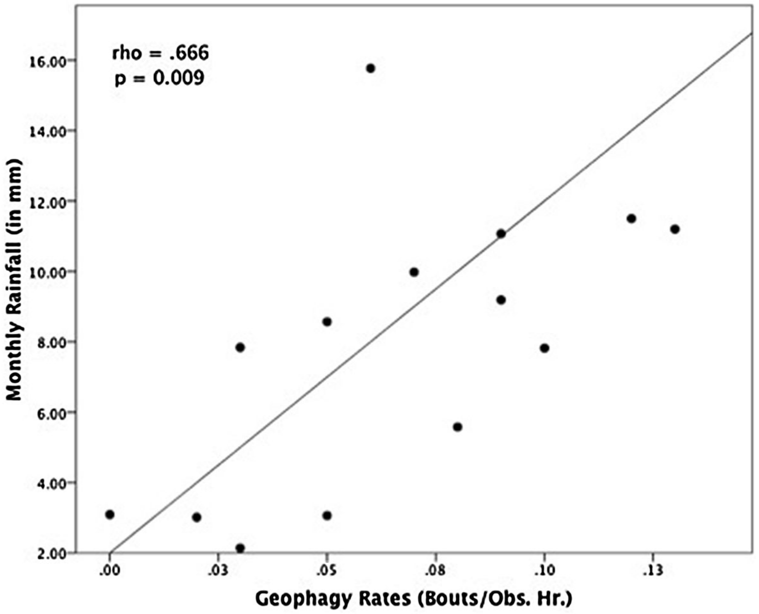

Fig. 2 Correlation between monthly rates of geophagy and rainfall during continuous sampling months from 2014 to 2015. Spearman's rank correlation coefficient (rho) and level of significance (*p*) are indicated within the graph

differences between sampled termitaria and topsoils (Table 4).

We then compared the samples from termitaria consumed by sakis ($N = 9$) with control samples ($N = 4$) from nearby termitaria that the monkeys bypassed and did not visit (Table 5). Consumed termitaria were more acidic than unconsumed termitaria ($\bar{x}_{\mathrm{used}} = 4.69 \pm$ SD 0.73 ppm, $\bar{x}_{\mathrm{unused}} = 5.71 \pm$ SD 0.52 ppm; corrected $P = 0.034$) and contained lower concentrations of P ($\bar{x}_{\mathrm{used}} = 335.61 \pm$ SD 108.45 ppm, $\bar{x}_{\mathrm{unused}} = 611.85 \pm$ SD 156.86 ppm; corrected $P = 0.019$). However, none of the other tested properties (EC, CEC, C %, Ca, Fe, K, Mg, Na) differed between samples from consumed and unconsumed termitaria.

Discussion

This study reports the first documented cases of geophagy in *P. rylandsi*, all of which occurred at arboreal termitaria. It is worth noting that the monkeys often visually inspected termitarium pieces, although the reason for this behavior is unclear. If the objective was primarily or solely consumption of termites, we would expect sakis to limit visits

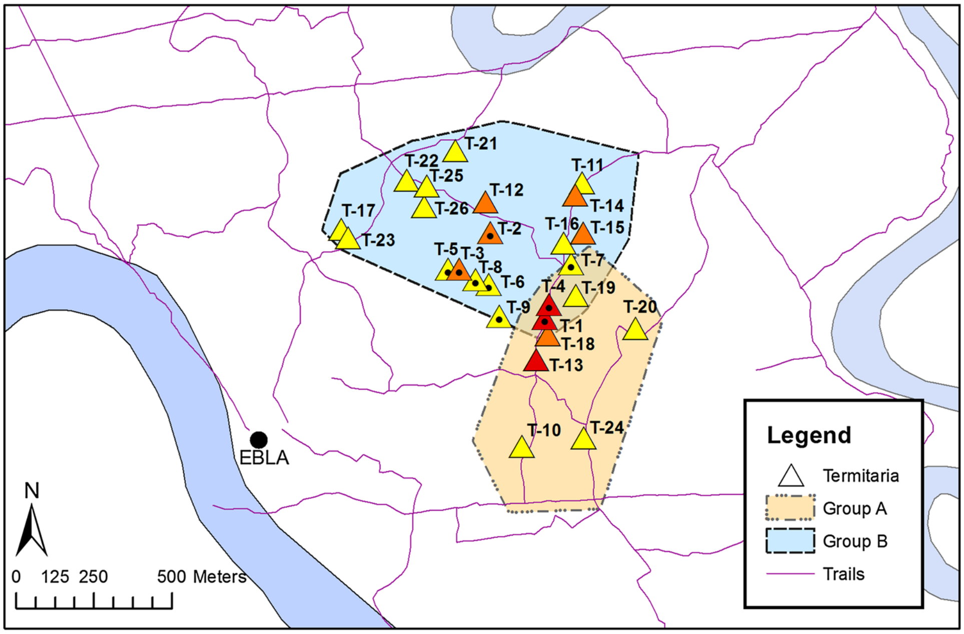

Fig. 3 Locations of termitaria (indicated as *triangles*) used as soil sources by *Pithecia rylandsi*. *Black dots inside triangles* indicate sampled termitaria. Termitaria are *color-coded* according to intensity of use; low use (1–2 visits) is indicated by *yellow*, medium use (3–7 visits) by *orange*, and high use (8+ visits) by *red*. The minimum convex polygons show the home ranges of each group

Table 3 Average compositions of termitarium soil and topsoil under termitarium

	Average composition		Mann–Whitney *U* test probability
	Topsoil ($N = 4$)	Termitarium soil ($N = 13$)	
ppm			
Ca	454 ± 72	1320 ± 941	0.017*
Mg	230 ± 43	559 ± 279	0.003*
Na	328 ± 40	354 ± 39	0.100
K	715 ± 174	1298 ± 465	0.009*
Fe	7656 ± 1809	9468 ± 3248	0.258
P	179 ± 90	467 ± 258	0.013*
Total C %	2.4 ± 1.3	5.8 ± 3.7	0.031*
pH (1:1)	3.5 ± 0.1	5.2 ± 0.8	0.003*
EC (dS/m)	0.4 ± 0.2	2.2 ± 1.6	0.213
Total CEC (meq/100)	8.8 ± 2.9	19.1 ± 8.4	0.006*

*Significant values ($P < 0.05$)

Table 4 Physical characteristics of termitarium soil and topsoil

	Topsoil ($N = 4$)	Termitarium soil ($N = 11^{a}$)	Mann–Whitney *U* test probability
Particle size (%)			
Sand	77.0 ± 8.6	70.9 ± 9.4	0.189
Silt	13.5 ± 1.0	14.8 ± 3.8	0.351
Clay	9.5 ± 4.4	14.3 ± 6.2	0.165

[a] Two termitaria samples were not analyzed for particle size

to inactive termitaria and spend more time feeding at active sites. However, the monkeys made repeated visits to inactive sites (in some cases over years) and did not stop feeding after sampling pieces without termites. In addition, feeding bouts were short, and there was no difference in the lengths of these events for active and inactive termitaria. This suggests that access to the soil itself was a function of the behavior. This consumption pattern is similar to

Table 5 Geochemistry for termitaria consumed by sakis and control/unvisited termitaria

Site	EC (ds/m)	Total CEC (meq/100 g)	pH (1:1)	C (%)	Ca	Exchangeable cations (ppm)				
						Mg	K	Na	Fe	P
T-1	1.52	21.92	4.52	7.7	2085.0	665.0	1025.0	355.0	6032.5	458.3
T-2	1.75	11.20	4.78	3.8	682.5	325.0	1055.0	300.0	9600.0	249.5
T-3	0.16	12.80	4.31	1.7	387.5	312.5	1082.5	350.0	13,950.0	253.5
T-4	2.10	12.48	5.69	5.6	1110.0	360.0	680.0	335.0	7002.5	325.8
T-5	0.62	26.72	3.81	8.0	1290.0	572.5	1295.0	400.0	12,900.0	478.4
T-6	0.18	13.92	3.99	1.7	460.0	322.5	1080.0	360.0	14,400.0	165.2
T-7	0.34	17.92	4.52	6.4	1272.5	527.5	1462.5	362.5	9225.0	277.6
T-8	1.86	20.80	6.01	7.5	1395.0	540.0	1297.5	362.5	10,625.0	438.2
T-9	0.36	14.08	4.60	5.3	857.5	475.0	1827.5	380.0	9825.0	374.0
C-1	0.36	9.60	4.95	2.4	607.5	472.5	1717.5	400.0	14,125.0	398.1
C-2	3.82	24.00	5.81	9.6	1835.0	757.5	1060.0	375.0	6495.0	602.8
C-3	3.02	28.32	6.00	8.0	2375.0	840.0	1995.0	390.0	7825.0	763.4
C-4	2.38	23.52	6.07	18.2	2175.0	675.0	962.5	345.0	6115.0	683.1
$\bar{x}_{\text{used}}$	0.99	16.87	4.69	5.30	1044.72	455.56	1200.56	356.11	10,395.56	335.61
SD_{used}	0.80	5.29	0.73	2.43	545.41	129.70	322.38	27.90	2912.74	108.45
$\bar{x}_{\text{unused}}$	2.40	21.36	5.71	9.55	1748.10	686.25	1433.75	377.50	8640.00	611.85
$\text{SD}_{\text{unused}}$	1.48	8.13	0.52	6.54	792.40	157.62	502.42	23.98	3729.44	156.86
P_{raw}	0.044	0.253	0.030	0.104	0.089	0.018	0.329	0.212	0.375	0.003
$P_{\text{corrected}}$	0.050	0.330	0.034*	0.106	0.148	0.504	0.710	0.260	0.414	0.019*

Raw P values were calculated using t-tests and corrected using stepwise Bonferroni correction

*Significant values ($P < 0.05$)

reported termitaria geophagy by *Alouatta belzebul*, which likewise was apparently not targeting the termites themselves as food (de Souza et al. 2002).

At 0.07 bouts per observation hour, geophagy rates for *P. rylandsi* were more than double the rates reported for other pitheciine species. Veiga and Ferarri (2007) reported that bearded sakis, *C. satanas*, in Brazil fed from two termitaria on only two occasions during a 4-year period (0.002 bouts/obs. h). Setz et al. (1999) observed 26 geophagy bouts on nine termitaria by golden-faced sakis, *P. pithecia chrysocephala*, in Brazil over 6 years (0.03 bouts/obs. h). Despite higher geophagy rates documented in our study population, the associated behaviors are remarkably similar to those reported in previous pitheciine studies. For example, feeding bouts by both *C. satanas* and *P. pithecia chrysocephala* were brief (~3 min). Individuals broke off small pieces from the mound or removed parts of the shelter tunnels and, in the case of *C. satanas*, placed mound material directly into the mouth. Similar to our findings, no age class or sex differences in frequency of geophagy were reported for these species.

Evidence for mineral supplementation

Mineral supplementation is often cited as a principal function of geophagy in primates due to high levels of minerals found in consumed soils. Our analyses show that termitaria soils consumed by *P. rylandsi* at EBLA contained higher concentrations of phosphorous, potassium, calcium, and magnesium than topsoil, which is consistent with findings by Setz et al. (1999) for *P. pithecia* in Brazil. In contrast, sodium and iron were not significantly higher in termitaria consumed by *P. rylandsi*, despite the association of these minerals with geophagy in other *Pithecia* species (*P. hirsuta*, Happel 1982; *P. pithecia*, Kinzey and Norconk 1993). We found no significant differences in mineral concentrations between consumed termitaria and nearby unconsumed termitaria, which suggests that the sakis were not preferentially targeting termitaria based on their higher mineral content. It is also possible that sakis avoided some termitaria based on the type of termite species that inhabited them. For example, *Alouatta seniculus* consumed soils from termite mounds constructed by *Constrictotermes* species while avoiding nearby mounds of *Labiotermes*, which may use chemical defenses that render these termitaria unpalatable (Izawa 1993). Thus, features of the termitaria that were not evaluated may have affected selection regardless of whether mineral supplementation was a function of the geophagy.

The importance of termitaria for mineral supplementation cannot be adequately determined without knowledge of a species' mineral requirements and availability of micronutrients from other dietary sources. Palminteri et al.

(2012) reported that 95.8% of the monthly diet of *P. rylandsi* at our study site consisted of fruit, with seeds alone accounting for 75% of frugivorous feeding observations. Data on nutritional content of seeds consumed by sakis is lacking; however, information on mineral content in seeds eaten by sympatric granivorous species may shed some light on nutrient availabilities. Gilardi and Toft (2012) documented mineral content in seeds eaten by three species of *Ara* macaws (*A. ararauna*, *A. chloropterus*, and *A. macao*) at two sites in Peru near EBLA. All four of the micronutrients (P, K, Ca, and Mg) that we found in high quantities in termitaria consumed by *P. rylandsi* are significantly more abundant in seeds consumed by *Ara* macaws. It is important to note that, while sakis and *Ara* macaws do feed on some of the same plant species, Palminteri et al. (2013) found that their diets overlapped by only 19%. However, sakis were also found to have a more taxonomically diverse diet consisting of plants from over 220 species (Palminteri 2010); thus they are able to acquire minerals from an even wider range of resources than macaws. Considering sakis' year-round diet of nutrient-rich seeds, we argue that mineral supplementation is likely not the primary or only function of geophagy in *P. rylandsi*. Data on their specific nutritional requirements are needed to determine what role, if any, mineral supplementation has in geophagy for the species.

Evidence for adsorption of dietary toxins

Given that pitheciids are known to exploit plant parts that contain high concentrations of secondary compounds, it is possible that sakis consume termitaria for a different physicochemical benefit: the adsorption or neutralization of toxins (Kinzey and Norconk 1993; Norconk et al. 1998). *P. pithecia* consume seeds with condensed tannins as high as >10% (Kinzey and Norconk 1993), which has led Norconk and Conklin-Brittain (2004) to conclude that sakis consume relatively high amounts of condensed tannins relative to their body weight. As has been shown in some animals (Klaus et al. 1998), consumption of soils with high clay content and CEC helps to detoxify tannins and other secondary compounds, because of their ability to bind or buffer against quinine and tannic acids (Gilardi et al. 1999; Brightsmith and Muñoz-Najar 2004). While our biochemical analysis revealed no differences in clay content between consumed and unconsumed termitaria, the CEC of consumed termitaria was more than twice as high as that of topsoil. Organic matter also has higher CEC, and the higher levels of carbon in termitaria compared to topsoil may relate to this higher CEC as well. This could be a factor in the sakis' use of termitaria in contrast to terrestrial soil sources. Termitaria consumed by *P. pithecia chrysocephala* also contained significantly higher CEC than topsoil or root mat; however, Setz et al. (1999) do not discuss these results in the context of tannin adsorption. While CEC of consumed soils has not been measured in other pitheciid studies, our findings confirm those of other studies on some granivorous psittacids. For example, Costa-Pereira et al. (2015) found high CEC in termitaria consumed by yellow-chevroned parakeets (*Brotogeris chiriri*) in Brazil and concluded that ingestion of termitaria was likely related to toxin binding for frugivorous vertebrates.

Setz et al. (1999) proposed that geophagy rates in sakis should be highest during peak fruit production if the primary function of geophagy is toxin adsorption. This hypothesis assumes that peak fruit production corresponds to higher fruit consumption and ingestion of more toxins. There is some seasonal variation in the diet of *P. rylandsi* at our study site, but it is less pronounced. Palminteri (2010) showed that sakis at EBLA consumed seeds from immature fruits year-round, including during peak fruit production in February and March. The only seasonal dietary shift noted was during the early dry season months of April and May. During this time, sakis consumed fewer seeds and instead relied heavily on ripe pulp from *Mauritia* palm fruits (Palminteri 2010). Our data show that geophagy rates for *P. rylandsi* are lowest during the early dry season periods of ripe fruit consumption and highest during the heart of the rainy season in January, when sakis are reported to consume seeds from immature fruits such as *Pouteria* and *Eschweilera* (Palminteri 2010). We were unable to conduct a biochemical analysis of foods consumed by *P. rylandsi*; however, Norconk and Conklin-Brittain (2004) documented higher levels of condensed tannins in young seeds than in ripe fruit pulp consumed by *P. pithecia* in Venezuela. Similarly, Gilardi and Toft (2012) found that seeds consumed by parrots in our study region contained tannins at levels considered to be extremely toxic to vertebrates (Gilardi and Toft 2012). Thus, our data indicate that soil consumption by *P. rylandsi* at EBLA likely function to mitigate the toxic effects of secondary compounds found in their year-round diet of seeds.

Conclusions

Regardless of the function of geophagy, it has been suggested that the importance of termitaria as a soil source for sakis is due to their accessibility in the forest matrix, which eliminates the need for the monkeys to descend to the ground where they may be more susceptible to predation (Ferrari et al. 2008). Predation risk has also been suggested to affect the selection of and behavior at geophagy sites by parrots (Burger and Gochfeld 2003). While *Pithecia* are highly arboreal and spend most of their time in mid- to high canopy, terrestrial activity has been widely reported among sakis (Barnett et al. 2012). Indeed, sakis at our field site occasionally descended to the ground to feed on army ants for periods of ∼1 h (Adams unpublished data). This indicates that certain terrestrial resources will attract sakis sufficiently to entice them to the ground, although arboreal access could still be an important feature of termite mounds over other soil sources.

In sum, our behavioral observations and soil analyses most strongly suggest that *P. rylandsi* consume soils from arboreal termitaria to aid in adsorption of toxins found in immature seeds, which are a year-round component of their diet. If mineral supplementation were the main driver of geophagy, then the occurrence of geophagy throughout the year would indicate that the saki monkeys' diet was consistently deficient or imbalanced in certain nutrients. The sakis' diverse diet and the lack of notable seasonal fluctuation in diet composition make this possibility less likely. Additional data on saki nutritional requirements and diet composition of micronutrients and secondary compounds are needed to further clarify the degree to which mineral supplementation and toxin neutralization play roles in geophagy for the species.

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Compliance with ethical standards

All applicable international, national, and institutional guidelines for the care and use of animals were followed. All research reported in this manuscript complied with reviews by Institutional Animal Care and Use Committees (IACUC) of Texas State University and Southern Illinois University Edwardsville, and followed protocols approved by The Ohio State University's IACUC. All protocols adhered to Peruvian legal requirements and were authorized by Peru's Ministry of Agriculture (MINAG).

Conflict of interest The authors declare no conflicts of interest.

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