ORIGINAL ARTICLE

Assessing the function of geophagy in a Malagasy rain forest lemur

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Abstract

Geophagy has been observed in nearly every long-term study of folivorous primates. Yet despite frequent observations of this behavior, conclusive explanations for soil consumption remain ambiguous. This study tests the most frequently proposed hypotheses for geophagy using data collected on the geophagic behavior of the Milne-Edwards' sifaka (*Propithecus edwardsi*) living in two forests with varying levels of disturbance within Ranomafana National Park, Madagascar. Field data were collected from December 2002 to November 2003, during which time soil samples were collected for mineral analyses from 102 sites selected for geophagy and 42 control sites at which no geophagy was recorded. Results indicate that control soils differ significantly between the two study sites and that this difference is primarily attributable to varying levels of habitat disturbance. The frequency of soil consumption also does not vary significantly by sex or between logged and unlogged habitats. Soil consumption significantly correlated with fruit/seed consumption overall, but to a lesser degree in logged compared with unlogged sites. Clay minerals found in soils likely prevent absorption of dietary toxins in the gut and/or may mediate gut pH. This provides strong evidence for the protection hypothesis for geophagy, which may be especially important in areas where logging, or other forms of habitat disturbance, has been experienced.

Abstract in French is available with online material.

KEYWORDS

habitat disturbance, Madagascar, primate, *Propithecus edwardsi*, Ranomafana National Park, sifaka, soil consumption

1 | INTRODUCTION

Geophagy, the intentional consumption of soil, is well documented in the mammalian, avian, and reptilian orders (*e.g.*, Gilardi, Duffey, Munn & Tell, 1999; Hladik & Gueguen, 1974; Klaus & Schmid, 1998; Sokol, 1971). In almost all reported cases, animals are highly selective in the soils consumed, frequenting specific consumption sites

that may even be outside of their typical home range (Best, Joseph & Goldizen, 2013; Pages, Lloyd & Suarez, 2005; Wiles & Weeks, 1986) and selecting particular soil horizons at feeding sites (Abrahams, 1999; Oates, 1978; Pages et al., 2005). Among wild primates, geophagy has been well-studied in Neotropical primates (Ferrari, Veiga & Urbani, 2008; Izawa, 1993), Old World monkeys (Mahaney, Milner & Sanmugadas, 1997; Oates, 1978; Wakibara et al., 2001), and great

apes (Mahaney, Hancock, Aufreiter & Huffman, 1996; Mahaney, Hancock, Aufreiter, Milner & Voros, 2016; Mahaney, Watts & Hancock, 1990), but remains poorly studied in Madagascar's lemurs (but see Ganzhorn, 1987; Norscia, Carrai, Ceccanti & Borgognini Tarli, 2005; Semel, 2015). A recent review on primate geophagy by Pebsworth, Huffman, Lambert and Young (2019) found 44 studies describing lemur geophagy, of which only five directly analyzed consumed soils. While most researchers agree that geophagy is typically an adaptive behavior, causes for geophagy remain poorly understood (Krishnamani & Mahaney, 2000; Pebsworth et al., 2019).

The main (nonexclusive) hypotheses for geophagy are the protection and supplementation hypotheses, as well as the nonadaptive hypothesis (Table 1). The protection hypothesis suggests that geophagy can alleviate symptoms of gastrointestinal distress (*e.g.*, Adams, Rehg & Watsa, 2017; Davies & Baillie, 1988; Ferrari et al., 2008; Mahaney et al., 1990; Oates, 1978; Setz, Enzweiler, Solferini, Amêndola & Berton, 1999; Wakibara et al., 2001) and protect consumers against parasites and pathogens (*e.g.*, Klein, Fröhlich & Krief, 2008; Knezevich, 1998; Mahaney & Krishnamani, 2003). The supplementation hypothesis suggests that geophagy supplements essential minerals that are lacking in the diet (*e.g.*, Heymann & Hartmann, 1991; Monaco et al., 2019; Reynolds et al., 2015). The nonadaptive hypothesis merely states that geophagy provides no physiological benefits, with hedonic sensation (Hladik & Gueguen, 1974; Voros et al., 2001) and culture or tradition (Mahaney et al., 1990) being the primary explanations for the behavior. However, very few studies have examined geophagic behavior within a population where study groups exist in habitats of significantly different quality (geographically or temporally), despite the likelihood that primates would alter soil consumption patterns to mediate dietary differences resulting from these differences. Of those who have, Reynolds et al. (2015) found evidence that chimpanzees consumed soil more frequently after the removal of forest palms that previously provided an important sodium source and Mahaney (1993) documented that

primates may prefer to take advantage of soils exposed by recent disturbance.

Habitat disturbance affects primate forage quality, as forest degradation reduces canopy cover, changes ambient forest temperature, and lowers native species diversity (Johns, 1986, 1992; Johns & Skorupa, 1987; Rice, Gullison & Reid, 1997). Soil nutrients and properties also are impacted by these factors (Kasenene, 1987; Schoenholtz, Van Miegroet & Burger, 2000; Struhsaker, 1997) as they increase precipitation reaching the forest floor (Kreutzweiser, Hazlett & Gunn, 2008; Powers et al., 2009) and decomposition and soil nutrient and mineral leaching rates (Lehman & Schroth, 2003). As such factors act in concert to affect populations' behavioral ecology, analyses of geophagy will be best understood when presented within a greater ecological context. Our study provides a natural experiment with which to examine the interactions between habitat disturbance, soil properties, and soil consumption within a rain forest-dwelling primate species.

Milne-Edwards' sifakas (*Propithecus edwardsi*) are the largest lemurs in Madagascar's southeastern rain forests (King et al., 2011; Wright, 1995). Madagascar has experienced high levels of habitat disturbance, fragmentation, and loss (Brown & Gurevitch, 2004; Vieilledent et al., 2018). Sifaka populations living in selectively logged and unlogged areas of Ranomafana National Park (RNP) have significant differences in their diet and potential nutrient intake (Figure 1; Arrigo-Nelson, 2006). Annually, sifakas living in logged forest consumed 16% less fruits/seeds than animals in unlogged forest. This difference is most significant during the austral winter months, when animals in unlogged forest spend up to 26% more time feeding on fruits/seeds than sifakas living in logged forest (Arrigo-Nelson, 2006). Given the nutritional differences between fruits, seeds, and leaves (*e.g.*, Altmann, Post & Klein, 1987; Arrigo-Nelson, 2006, Donati et al., 2017; Ganzhorn et al., 2017; National Research Council 2003), sifaka diets in logged forest likely contain not only fewer sugars and fats, but also fewer plant secondary metabolites (PSMs) from

TABLE 1 Frequency of feeding, identity of animals feeding, and soil types consumed, as predicted by each proposed hypothesis for geophagic behavior

Hypothesis	Corollary	Geophagy		
		Frequency	**Feeders**	**Soil type**
Protective	Digestive function	Frequent or predictable	All	Higher pH than stomach contents
	Toxin neutralization	Frequent[a]	All that consume toxins	Contain kaolin or other absorptive properties
	Self-medication	Periodic[a]	Those infected or showing symptoms	Contain kaolin or other absorptive properties
	Ingest cellulose digesting bacteria	Rare to frequent	All	Taken from termite mounds
Dietary Supplementation	Dietary supplementation	Rare or occasional	All or those with increased nutritional needs	Contain nutrient(s) absent from diet or present in low quantities
Nonadaptive	Famine food	Rare	All	Nutrient-rich soils
	Cultural adaptation/tradition	Rare to frequent	Possibly all	Variable
	Tactile sensations/olfactory attraction	Rare to frequent	All	Variable

[a]may occur only seasonally.

seeds than those in unlogged forest due to the lower proportion of fruits and seeds in their diet. PSMs, such as toxins (*e.g.*, alkaloids) and protein inhibitors (*e.g.*, tannins), may cause animals physiological harm or inhibit protein intake—costs that must be weighed against the nutritional benefits of a particular food item (Glander, 1982). As nutritional differences are most significant during the winter (lean season and sifaka birth/early lactation season), this combination of high-energy demands, a lack of high-energy foods, and PSM prevalence could severely impact sifakas in logged forest.

Sifaka life history and diet have been studied over 30 years in RNP (Arrigo-Nelson, 2006; Hemingway, 1995, 1998; King et al., 2011; Morelli, King, Pochron & Wright, 2009; Wright, 1995), and based on these observations, it is feasible that sifaka geophagy could conform to any of the three main geophagy hypotheses (Table 1). By closely examining geophagy patterns among sifakas, this study will improve our understanding of the root cause(s) of soil consumption

within this species and contribute to the general understanding of this phenomenon, not just among lemurs, but among all primates. Further, as differences exist in the feeding ecology of sifakas living within selectively logged and unlogged forest, this study also provides an opportunity to explore the impact of habitat disturbance on the sifakas of RNP and the ways that geophagy may help animals persist in logged habitats.

2 | METHODS

2.1 | Study sites

Ranomafana National Park (RNP) encompasses 43,500 ha of rain forest in southeastern Madagascar (21°02'–21°25'S and 47°18'–47°37'E). Elevation ranges from 500 m to 1500 m, and habitat varies with elevation, changing from lowland to montane rain forest.
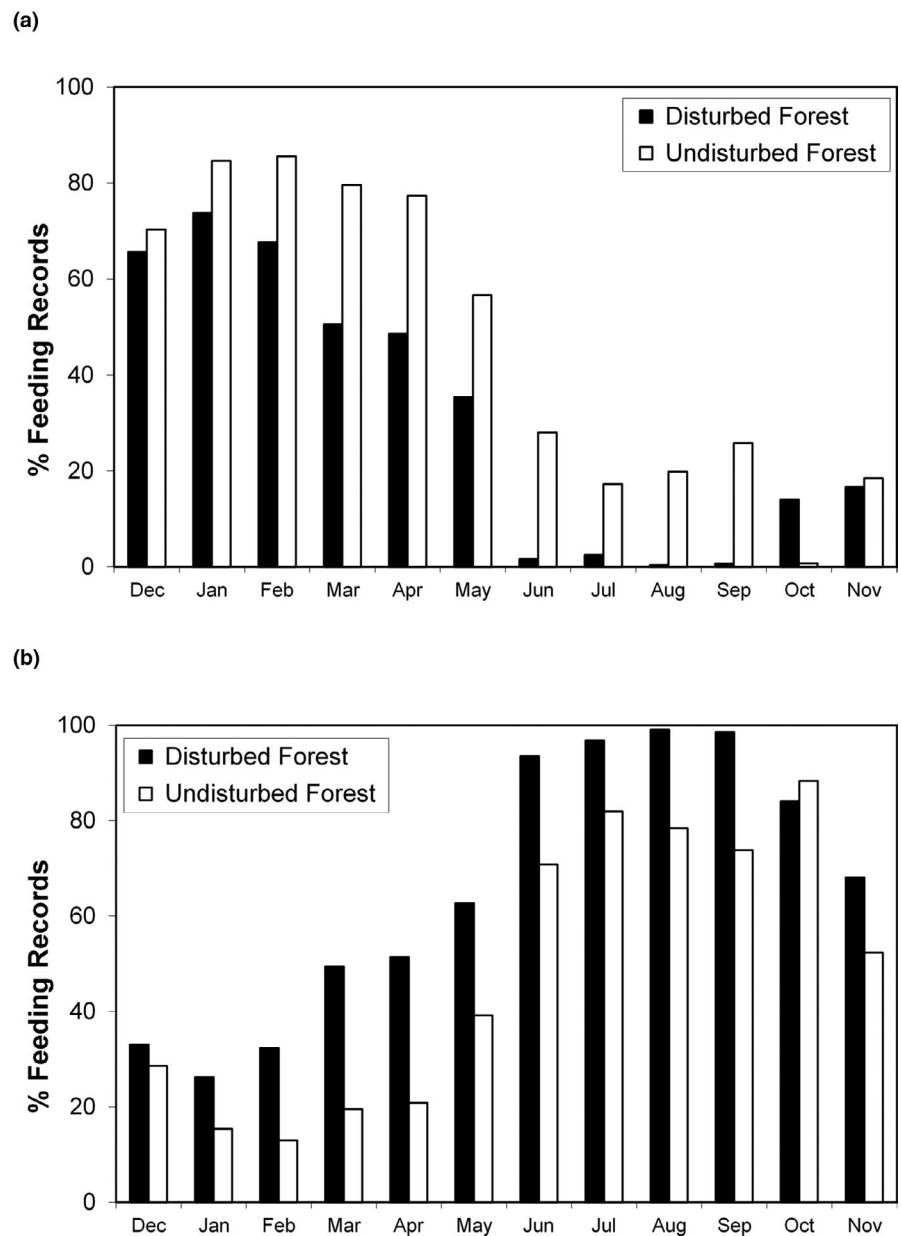
(a)

(b)

FIGURE 1 Monthly variation in (a) fruit and (b) leaf consumption by sifakas in undisturbed and disturbed forest, throughout the study period

The region's climate is both seasonally and interannually variable (Eronen, 2017; Wright et al., 2012). Rainfall averages 3,400 mm per year, though half of this total fell in just 3 months (January–March) in 2003, and temperatures ranged between 6.5°C and 30°C during this same period (Arrigo-Nelson, 2006). This study focuses on sifakas inhabiting two of RNP's trail systems, which were selected for their past logging histories (Figure S1). The logged forest site, Talatakely, is 850 m to 1150 m asl, contains a trail network over 30 km in length, and encompasses 1.5 km². Of the established trail systems, this site has been subjected to the greatest level of habitat disturbance, including the presence of a small settlement and market from the early 1930s to 1947 and intensive "selective" logging by timber exploiters from 1986 to 1989 (Wright, 1997; Wright et al., 2012). During peak exploitation, approximately 300 hardwood trees were hand-removed from the area daily, including several key sifaka food species. The unlogged forest site, Valohoaka, is 8.5 km southeast of Talatakely. This system is 900 m to 1200 m asl, consists of 21.5 km of trails, and encompasses 1.41 km². This site has been impacted by neither human settlements nor selective logging (Balko & Underwood, 2005).

2.2 | Study species and groups

Milne-Edwards' sifakas are diurnal, sexually monomorphic, and the largest lemur species in RNP, with adult body weights averaging 5.8 kg (Figure S2; Glander, Wright, Daniels & Merenlender, 1992; King et al., 2011). Social groups range from 2 to 9 animals (Pochron & Wright, 2003) and maintain 30 to 55 ha home ranges (Gerber, Arrigo-Nelson, Karpanty, Kotschwar & Wright, 2012). Their diet consists of a combination of leaves, whole fruits, and seeds, and varies seasonally with animals preferentially feeding on available fruits and seeds (Arrigo-Nelson, 2005, 2006; Hemingway, 1998; Wright, 1995). Flowers and insect larvae seasonally supplement diets. Drinking water has never been observed in over 20 years of sifaka research at this site. Data presented here have been collected from seven sifaka groups, four from the logged forest (18 individuals) and three from the unlogged forest (11 individuals) that were observed from December 2002 to November 2003 (Table S1). The simultaneous study of these seven groups enables behavioral and ecological comparisons between sites with differing levels of habitat disturbance, while controlling for within-site variation.

2.3 | Data collection

Soil samples were collected in two contexts: "consumed" and "control." *Consumed* soils were collected during sifaka observations conducted from December 2002 through November 2003. Each sifaka group was followed from dawn to dusk for four or five consecutive days each month by a three-member team (some combination of Arrigo-Nelson and the project's six Malagasy research technicians). A total of 3,397 observation hours were logged (393–526 hr collected per group). During group follows, all geophagy events and locations were documented. Following each feeding event, a soil sample (approximately 150 g wet weight) from the feeding location was collected in a cloth forestry bag, dried in a drying oven at 40°C for 2 weeks, and then stored in a Ziploc® bag containing Dry Rite® desiccant until nutrient/mineral analyses were conducted. Samples contained no sizeable debris (i.e., roots, leaves, and large stones). *Control* soils were collected from the study's established botanical plots in November 2003. Six botanical plots were established within each study group's home range following the stratified random sampling methodology of Mueller-Dombois and Ellenberg (1974), in which plots were placed randomly within each group's home range but in proportional distribution to the habitat types found therein (Hsu, Agoramoorthy & Lin, 2001; Müller, Ahl & Hartmann, 1997). Within each botanical plot, 125 cm³ of soil was collected from a homogenized core sample of the first 25 cm of soil from the first quadrant of each plot. Roots, leaf litter, and the O horizon were removed, as they were not consumed by the sifakas. Samples then were dried and preserved as described above.

2.4 | Laboratory analyses

Soil properties were determined for each sample using two independent analyses: a standard soil analysis and a soluble ion analysis by the Soil and Plant Testing Laboratory (University of Massachusetts-Amherst) in 2004. Soil analyses were conducted using Morgan extraction, a standard acid-extraction method used in soil sciences (1:2, soil:water extraction; Lunt, Swanson & Jacobson, 1950; NEC-67, 1995) to quantitatively determine extractable micronutrient, heavy metal, and organic matter content, and pH values. Soluble ion analyses were used to determine the soluble salt content of the soils. As the nature of these analyses differs, the tests
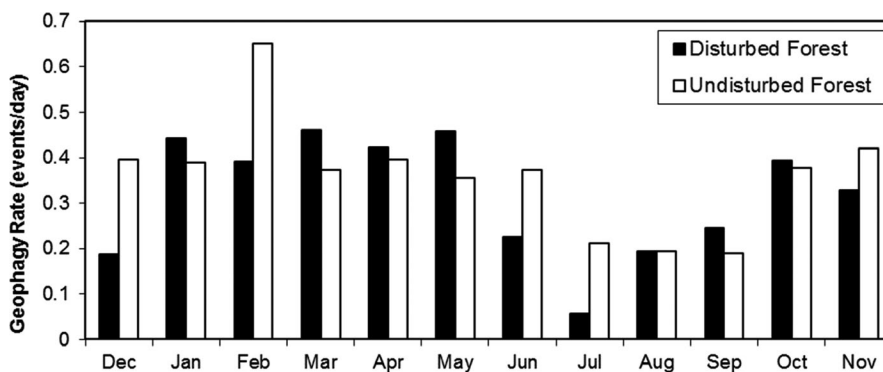

FIGURE 2 Monthly variation in geophagy rate by sifaka in undisturbed and disturbed forest, throughout the study period. No significant differences were found among months, between forest types

are considered complementary and can be interpreted in concert to determine soil properties and differences between control soils and those consumed by sifakas (S. Bodine, *pers. comm.*).

2.5 | Statistical analyses

As all weaned members of a social group routinely participated in each geophagic event, the consumption event itself was taken as the sampling unit (not the soil feeding bouts of individual group members). Due to unequal sample sizes, non-normal distribution of means, and nonindependence between *consumed* and *control* soils at each site, a combination of parametric and nonparametric analyses was used (Sokal & Rohlf, 2012). Kruskal–Wallis tests were employed with Dunn–Bonferroni post hoc analyses to explore differences in soil texture and properties within and between sites. Soil texture values (%) were arcsine-transformed prior to analysis. Paired sample *t*-tests were used to investigate differences in the rate of geophagy within and between sites. Pearson correlations were used to determine the relationship between geophagy and fruits/seeds feeding within each study site, across the study period, and Fisher's combined probability test was used to test the overall significance of this relationship across study sites. Probabilities were combined using the formula: $T = -2\_\ln(p)$, where T is chi-square distributed with four degrees of freedom (df = 2n; n equals the number of data sets included). All analyses were conducted using SPSS v. 22.

3 | RESULTS

3.1 | Geophagic behavior

Overall, geophagy was observed 102 times, with 44 events (0.032 events/hr or 0.317 events/day) occurring within unlogged forest and 58 events (0.028 events/hr or 0.317 events/day) occurring within logged forest. The ingestion method was stereotypical across all individuals at both sites as follows: Geophagic events followed the intentional/directed travel of a social group to a location when no other reason for travel to this site or away from their previous location could be discerned. During each event, all weaned individuals of both sexes consumed soil. Group members descended to the ground sequentially. Adult females led and other group members followed one-by-one. Adult males went last. Once on the ground, animals consumed two to three mouthfuls of soil from the selected area using only their mouths before immediately leaving the feeding site. While waiting to feed, animals rested low in the trees (<10 m), gave frequent contact calls, and were noticeably vigilant. After all individuals had fed, the group traveled rapidly from the site before engaging in any further feeding or resting behaviors.

Soils were exclusively consumed from sites lacking an A horizon (dark, humus layer containing leaf litter, decayed materials, and other organics) where the more compact B horizon (lighter/orange in color) soils had been previously exposed (i.e., due to a treefall or cliff erosion) and were free of debris (*e.g.*, roots, leaves, and stones). Throughout the course of this study, 36 geophagy sites were used

within the unlogged forest and 49 sites were used in the logged forest. On average, these sites were reused 1.33 times within the unlogged forest and 1.40 times within the logged forest, with 37.50% of sites visited more than once (maximum four times) within the unlogged forest and 52.83% of sites revisited (maximum three times) within the logged forest.

When soil consumption rates were compared between sites, no difference in geophagy rate was found ($p = .087$) within any study month ($n = 12$; Figure 2). Geophagic behavior was significantly correlated with fruit/seed consumption within the unlogged forest (Pearson's $r = .584$, $p = .046$) and trended toward a correlation within the logged forest (Pearson's $r = .544$, $p = .068$) as well. Fisher's combined probability suggested a highly significant relationship between geophagic behavior and fruit/seed consumption across sites ($T = 11.53$, $p < .025$; Figure 3).
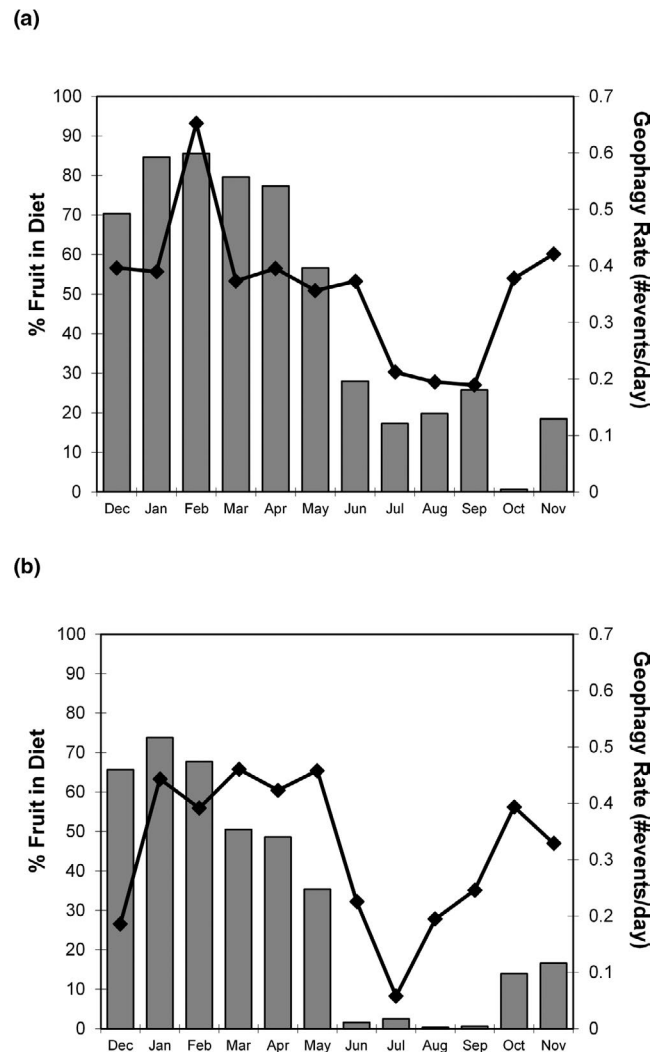
(a)

(b)

FIGURE 3 Monthly geophagy rate and proportion of diet consisting of fruit/seeds for sifakas living in (a) the undisturbed and (b) the disturbed forest study sites. Fisher's combined probability test reveals that across sites, geophagy and fruit feeding are significantly correlated ($p < .025$)

TABLE 2 Soil properties and nutrient content of control (collected from randomly distributed botanical plots) and chosen soil samples (collected from sifaka feeding sites). Undisturbed forest = Valo and disturbed forest = Tala. Mean values and standard deviations presented here. Significance values calculated using Kruskal–Wallis tests, with Dunn–Bonferroni post hoc comparisons.

	H	p-value	Undisturbed (Valo)			Disturbed (Tala)			Post Hoc Comparisons	
			Control	Chosen	Post Hoc	Control	Chosen	Post Hoc	TALA vs. VALO Control	TALA vs. VALO Chosen
Soil Composition (%)										
Sample size:	48		11	3		22	12			
Sand	25.11	<0.001	83.34 ± 3.81	87.47 ± 5.69	n.s.	77.73 ± 7.34	65.47 ± 7.68	$z = -16.13\ p = .008$	n.s.	$z = -32.50\ p = .002$
Silt	13.97	0.003	12.10 ± 4.06	9.03 ± 4.44	–	15.30 ± 6.59	20.74 ± 4.52	n.s.	–	$z = 25.25\ p = .031$
Clay	14.51	0.002	4.56 ± 3.98	3.50 ± 1.55	n.s.	6.96 ± 5.42	13.79 ± 6.65	$z = 14.25\ p = .027$	n.s.	$z = 22.17\ p = .085$
Standard soil analyses (mg/kg)										
Sample size:	144		16	44		26	58			
% Nitrogen[a]	2.22	0.027	0.43 ± 0.11	–	–	0.36 ± 0.08	–	–	–	–
pH	11.15	0.011	4.50 ± 0.26	4.53 ± 0.34	n.s.	4.74 ± 0.30	4.65 ± 0.30	n.s.	$z = 33.63\ p = $ **.065**	n.s.
Soluble Salts	27.72	<0.001	0.34 ± 0.06	0.36 ± 0.14	n.s.	0.25 ± 0.06	0.26 ± 0.08	n.s.	$z = -42.02\ p = .009$	$z = -34.82\ p < .001$
Organic Matter	32.46	<0.001	16.01 ± 3.52	13.13 ± 4.49	$z = -32.09\ p = $ **.05**	12.68 ± 3.09	10.28 ± 2.87	$z = -28.80\ p = .021$	n.s.	$z = -29.38\ p = .003$
Nitrate	30.37	<0.001	16.94 ± 3.19	12.11 ± 7.31	$z = -40.87\ p = .005$	9.04 ± 4.32	9.40 ± 7.72	n.s.	$z = -56.81\ p < .001$	n.s.
Ammonium	10.10	0.018	24.56 ± 5.18	41.80 ± 25.57	n.s.	21.31 ± 4.51	32.48 ± 23.40	n.s.	n.s.	n.s.
Aluminum	2.01	n.s.	229.98 ± 44.05	213.30 ± 80.54	–	241.52 ± 110.53	217.81 ± 75.49	–	–	–
Boron	10.41	0.015	0.11 ± 0.04	0.12 ± 0.04	n.s.	0.11 ± 0.03	0.10 ± 0.04	n.s.	n.s.	$z = -26.67\ p = .008$
Cadmium	24.37	<0.001	0.01 ± 0.01	0.04 ± 0.02	$z = 55.80\ p < .001$	0.04 ± 0.03	0.04 ± 0.02	n.s.	$z = 44.39\ p = .004$	n.s.
Calcium	16.98	0.001	109.04 ± 162.50	74.99 ± 39.92	n.s.	92.99 ± 116.02	51.54 ± 43.95	n.s.	n.s.	$z = -33.05\ p < .001$
Chromium	9.50	0.023	0.16 ± 0.07	0.18 ± 0.11	n.s.	0.15 ± 0.07	0.22 ± 0.12	$z = 27.95\ p = .027$	n.s.	n.s.
Copper	0.67	n.s.	0.35 ± 0.15	0.34 ± 0.19	–	0.35 ± 0.15	0.34 ± 0.17	–	–	–
Iron	15.23	0.002	44.11 ± 29.73	37.60 ± 24.99	n.s.	34.06 ± 21.54	24.73 ± 16.38	n.s.	n.s.	$z = -24.74\ p = .018$
Lead	18.80	<0.001	0.81 ± 0.51	1.41 ± 0.52	$z = 42.04\ p = .003$	1.44 ± 0.60	1.54 ± 0.62	n.s.	$z = 42.51\ p = .008$	n.s.
Magnesium	39.50	<0.001	85.27 ± 63.10	49.37 ± 25.27	$z = -32.10\ p = $ **.05**	68.88 ± 34.51	34.54 ± 23.38	$z = -49.26\ p < .001$	n.s.	$z = -26.02\ p = .011$
Manganese	1.02	n.s.	15.54 ± 16.56	19.57 ± 20.78	–	22.71 ± 23.76	17.77 ± 16.41	–	–	–
Nickel	8.29	0.040	0.08 ± 0.09	0.10 ± 0.06	n.s.	0.12 ± 0.06	0.09 ± 0.06	n.s.	n.s.	n.s.
Phosphorus	12.29	0.006	5.26 ± 2.11	10.03 ± 8.25	$z = 35.87\ p = .019$	5.76 ± 1.91	6.78 ± 3.49	n.s.	n.s.	n.s.
Potassium	21.32	<0.001	76.92 ± 21.91	68.47 ± 32.67	n.s.	64.88 ± 21.06	55.16 ± 43.95	$z = -28.83\ p = .020$	n.s.	$z = -27.31\ p = .006$
Zinc	92.08	<0.001	6.03 ± 2.39	0.64 ± 0.28	$z = -66.26\ p < .001$	5.28 ± 2.15	0.51 ± 0.21	$z = -76.77\ p < .001$	n.s.	n.s.

(Continues)

3.2 | Soil properties and chemistry

Soil properties differed significantly between unlogged and logged *control* samples for only a few measures (Table 2). Unlogged forest soils contained significantly higher levels of soluble salts ($p = .009$) and standard nitrate ($p < .001$). Logged forest soils exhibited higher levels of cadmium ($p = .004$) and lead ($p = .008$) and tended to have a higher pH ($p = .065$, *n.s.*) than unlogged forest soils.

When comparing *consumed* and *control* soil chemistry within sites, several differences were found (Table 2). In logged forest, *consumed* soils had a significantly higher clay ($p = .008$) and chromium ($p = .027$) content than *control* soils. Within unlogged forest, *consumed* soils contained significantly more cadmium ($p < .001$), lead ($p = .003$), and phosphorus ($p = .019$), and significantly less nitrate ($p = .005$) than *control* soils. Organic matter tended to be lower as well ($p = .050$, *n.s.*). At the logged forest site, *consumed* soils contained significantly less sand ($p = .027$) and standard potassium ($p = .020$) than *control* soils. Additionally, when the *consumed* soils were compared to *control* soils, several patterns emerged that were common to both sites. *Consumed* soils consistently (1) had a trend toward lower organic matter content (Valo: $p = .050$, *n.s.*, Tala: $p = .021$); (2) contained significantly less zinc (both sites: $p < .001$) and tended to contain less magnesium (Valo: $p = .050$, *n.s.*, Tala: $p < .001$); and (3) contained significantly more soluble manganese ions (Valo: $p = .014$, Tala: $p = .027$) and significantly fewer soluble zinc ions (both sites: $p < .001$) than *control* sites.

Between sites, *consumed* soils from the logged forest had significantly higher sand ($p = .002$) and silt ($p = .031$) content than those in the unlogged forest. *Consumed* soil clay content also tended to be different between sites ($p = .085$, *n.s.*). *Consumed* soil comparisons differed significantly between sites for nearly half of the measured micronutrients (Table 2).

4 | DISCUSSION

Here, we present one of the first systematic studies of soil consumption in wild lemurs and investigate the adaptive significance of geophagy by Milne-Edwards' sifakas under natural experimental conditions across a full seasonal spectrum using robust sample sizes. These conditions, along with control samples, are often lacking in anecdotal geophagy reports. Comparative studies of geophagy between populations facing dissimilar habitat qualities and nutritional landscapes provide a noninvasive and non-reductionist approach to explain the function of soil within primate diets. In this study, *control* soil samples collected within animal home ranges enable the characterization of soils across disturbance regimes and a critical investigation of preferred soil properties.

4.1 | General findings

Previous deforestation response studies suggest soil nitrates decrease due to vegetation loss and erosion, which can reduce soil

TABLE 2 (Continued)

	H	p-value	Undisturbed (Valo) Control	Chosen	Post Hoc	Disturbed (Tala) Control	Chosen	Post Hoc	Post Hoc Comparisons TALA vs. VALO Control	TALA vs. VALO Chosen
Soluble Ion analyses (mg/l)										
Sample size:	138		16	39		26	57			
Aluminum	5.63	n.s.	8.51 ± 2.74	16.51 ± 18.15	–	8.67 ± 3.97	8.76 ± 6.58	–	–	–
Boron	21.43	<0.001	0.08 ± 0.03	0.09 ± 0.04	n.s.	0.06 ± 0.02	0.06 ± 0.02	n.s.	n.s.	z = −31.29 p = .001
Calcium	21.13	<0.001	7.00 ± 5.89	12.11 ± 8.80	z = 30.61 p = **.06**	5.65 ± 4.03	7.11 ± 4.99	n.s.	n.s.	z = −28.52 p = .004
Iron	11.18	0.011	2.69 ± 1.42	4.74 ± 5.43	n.s.	2.93 ± 1.46	2.42 ± 1.74	n.s.	n.s.	z = −25.75 p = .012
Magnesium	20.86	<0.001	7.67 ± 5.48	11.46 ± 8.97	n.s.	4.86 ± 2.59	6.00 ± 5.57	n.s.	n.s.	z = −33.97 p < .001
Manganese	17.29	0.001	1.17 ± 1.72	4.54 ± 7.04	z = 36.01 p = .014	1.20 ± 1.29	3.85 ± 4.86	z = 26.88 p = .027	n.s.	n.s.
Phosphorus	13.49	0.004	2.11 ± 1.34	2.56 ± 3.03	n.s.	1.74 ± 0.98	1.30 ± 1.05	n.s.	n.s.	z = −22.00 p = .049
Potassium	18.94	<0.001	29.80 ± 9.80	28.14 ± 13.27	n.s.	22.80 ± 9.62	20.52 ± 10.04	n.s.	n.s.	z = −28.74 p = .003
Zinc	48.22	<0.001	0.22 ± 0.09	0.11 ± 0.10	z = −47.93 p < .001	0.16 ± 0.09	0.07 ± 0.05	z = −47.54 p < .001	n.s.	n.s.

[a]% Nitrogen analyzed using a Mann–Whitney U test, so test statistic presented is Z, not H.
Values approaching significance are bold.

acidity for years or decades until regeneration is achieved (Li et al., 2013; Reiners, Bouwman, Parsons & Keller, 1994; Werner, 1984). This study conforms to this trend with soil containing lower nitrates and higher pH in logged versus unlogged forest sites. Although several important minerals also were found in lower concentrations in logged verses unlogged forest soils, few differences were statistically significant (Table 2). While tropical forests typically are infertile and poor in minerals (Li et al., 2013; Werner, 1984), we expected to see many notable differences in soil properties between the two sites. Selective logging, rather than a total clear-cut, may have buffered the logged site against intense mineral leaching. Alternatively, soil recovery may have occurred rapidly due to the presence of the contiguous forest trees lacking value to the commercial logging trade. Either scenario is good news for soil conservation in RNP's logged areas, and the latter scenario may provide limited support for the use of selective logging to mitigate damage in regions where cutting is scheduled to occur.

Sifaka behavior at geophagy sites suggests that the animals may feel vulnerable to terrestrial predators (e.g., fossas) while consuming soil. Like spider and howler monkeys visiting mineral licks (Link, Galvis, Fleming & Di Fiore, 2011), sifakas exhibited increased vigilance while at geophagy sites. Though sifakas did not spend long periods at sites prior to descending to the ground, they did take turns feeding and maintained regular contact calls at geophagy sites. While small exposed soil sites may have prevented communal feeding bouts, turn taking was ubiquitous and likely enabled consumers to benefit from vigilant group members.

When our results are examined in light of the three major hypotheses for geophagy, we find the following:

4.2 | Protection hypothesis

The protection hypothesis may be supported by any number of several nonexclusive corollaries explaining the function of soil in the diet including defense against plant secondary metabolites (PSMs), adjustment of gut pH, and defense against parasites and pathogens (Table 1; Krishnamani & Mahaney, 2000; Pebsworth et al., 2019).

The capacity for consumed clays to neutralize various PSMs has been well supported across the geophagy literature (Gilardi et al., 1999; Houston, Gilardi & Hall, 2001; Setz et al., 1999; Wakibara et al., 2001). PSMs are compounds that are secondary to a plant's cellular function, but that discourage predation by herbivores by either negatively impacting their physiology (e.g., toxins) or inhibiting protein absorption (e.g., tannins; Glander, 1982). Clay minerals from consumed soils are known to increase mucous production, thereby reducing the permeability of the intestinal lining and/or to bind to PSMs directly to facilitate their excretion (reviewed in Young, 2010). While this function was first attributed to folivores dealing with high toxin concentrations in mature leaves (Krishnamani & Mahaney, 2000), more recent reviews of geophagy suggest a strong link to frugivory due to toxic seeds (Ferrari et al., 2008; Pebsworth et al., 2019). We found that soil consumption significantly correlated with fruit/seed consumption in unlogged forests and to a lesser degree in

logged forests, with a high correlation between fruit/seed consumption and geophagy overall (Figure 3).

Sifakas are known seed predators, sometimes discarding fruit pulp to feed exclusively on seeds (Dew & Wright, 1998). In Mantadia National Park, more granivorous diademed sifakas consumed soil twice as often as more folivorous indris, strongly implicating detoxification as the function of geophagy (Powzyk & Mowry, 2003). Seeds consumed by diademed sifakas were rich in alkaloids (e.g., from the genus Solanum, also consumed by Milne-Edwards' sifakas (Arrigo-Nelson, 2006)), while foods consumed by sympatric indri were not. Additionally, Semel (2015) provided evidence that diademed sifakas were more likely to consume soil within 12- and 30-hr periods (based on sifaka gastric emptying and oro-rectal transit times) with higher food toxin indices than those with lower indices. Norscia et al. (2005) also suggested detoxification as a likely explanation for geophagy in Verreaux's sifakas.

Soils also may help to adjust gut pH. Like most animals that engage in geophagy, sifakas at both sites consistently avoided soil organic matter (Table 2; Klaus & Schmid, 1998). Consequently, sifakas consistently chose less acidic soils. Clays typically are thought to be the buffering agent (Mahaney et al., 1990; Semel, Irwin, Raharison, Chapman & Rothman, 2014; Wakibara et al., 2001). Ruminants and ceco-colic fermenters, such as sifakas, support an array of symbiotic bacteria that break down plant materials (e.g., cellulose) through fermentation (Campbell, Eisemann, Williams & Glenn, 2000; Chivers & Langer, 1994; Lambert, 1998). These bacteria function best in more neutral environments than the acidic conditions of the gastrointestinal tract. Clays in consumed soils may act to reduce gut pH, creating a more favorable fermentation environment (Davies & Baillie, 1988; Oates, 1978; Wakibara et al., 2001). Logged forest consumed soils had significantly more clay than control soils, but this was not the case in unlogged forest. Consumed soils between sites were not significantly different from one another.

Sifaka feeding patterns and lack of sex and age bias in soil consumption also lend support to geophagy as a means to alleviate toxins or to adjust gut pH. Geophagy is correlated with fruit/seed consumption at both sites. Soil was consumed seasonally, with sifakas feeding on soil frequently during peak fruiting season (December–May) and decreasing consumption when fruit/seed consumption was at its lowest (June–September; Figure 3).

Geophagy also may help primates to improve their physical condition by protecting against parasites and pathogens (Huffman & Seifu, 1989). Certain clay minerals from consumed soils are known to reduce the permeability of the intestinal lining to filter out toxins and pathogens and to bind to pathogens directly to facilitate excretion (reviewed in Young, 2010). Rhesus macaques on Cayo Santiago routinely consumed soil, enabling them to avert external symptoms of infection, such as diarrhea. This allowed hosts and parasites to reach a level of homeostasis in which physical condition, reproductive status, and longevity were not compromised (Knezevich, 1998).

Our data did not fully support this corollary of the protection hypothesis. Though geophagy was most frequent during seasons when parasites are more prevalent (Wright et al., 2009), geophagy rates were similar between logged and unlogged forests despite

sifakas in more logged habitats having higher endo- and ectoparasite loads than those in unlogged forest (Bublitz et al., 2015; Wright et al., 2009). While we cannot completely reject the role of geophagy in protecting against sifaka parasites, the toxin alleviation and adjustment of gut pH corollaries provide the best support for the protective hypothesis.

One potential corollary of the protective hypothesis that we were unable to test with our data is the role of geophagy as a pre- or probiotic. A review by Bisi-Johnson, Obi and Ekosse (2013) found that clays in soil may inhibit certain harmful microbes, while the soil itself acts as a source for beneficial gut microbes. This corollary has received little attention in the literature and may warrant future exploration owing to the complex gut morphology and symbiotic relationship between sifakas and their gut flora.

4.3 | Supplementation hypothesis

Dietary supplementation is a well-accepted explanation for primate geophagy (Table S2). While Madagascar's lemurs face unique nutritional challenges (Donati et al., 2017; Wright, 1999), geophagy patterns similar to those of other primates persist. Like sifakas, Formosan macaques exhibit no age or sex bias in soil consumption and annually consume soil from numerous sites (Hsu et al., 2001). Unlike for sifakas, peak macaque soil consumption occurred at the end of the rainy season and continued through the dry season, largely corresponding to high folivory periods. Because soil consumption was observed among sifakas of all ages and of both sexes, it is possible that they must consume soil to supplement mineral(s) generally lacking in their diets. Of the minerals sampled, only soluble manganese ions were significantly higher in soils *consumed* by sifakas than in *control* soils for both forest types.

Manganese ions are a trace element and biologically necessary in small quantities. They are required for bone, cartilage, skin, and ligament formation, reproductive and brain function, blood clotting and wound healing, and cholesterol, sugars, and insulin metabolism (Dreosti, 1992; Medline Plus 2016). Several enzymes activated by manganese contribute to the metabolism of carbohydrates, amino acids, and cholesterol (Medline Plus 2016). Sifakas may not be able to ingest enough manganese in their regular diet. Humans only absorb 3–9% of consumed manganese (Sandstöm, 1992), while some herbivores only absorb 1% of consumed manganese (cf. Spears, 2003).

The absence of mineral analyses in studies of the Milne-Edwards' sifaka diet makes it impossible to test whether or not these sifakas have a manganese deficiency. However, while related diademed sifakas living in similar forest habitats failed to meet National Research Council recommendations for calcium, copper, iron, sodium, phosphorus, and zinc, they exceeded potassium, magnesium, and manganese recommendations (Irwin, Raharison, Chapman, Junge & Rothman, 2017).

We also observed site-specific preferences unrelated to underlying soil mineral differences. *Consumed* soils from logged forest had less potassium than *control* logged forest soils and *consumed* unlogged forest soils. Unlogged forest *consumed* soils contained more

nitrate, cadmium, lead, and phosphorus than *control* samples, but there was no difference in *consumed* soils between the two forest types. Additionally, logged forest *consumed* soils were consistently lower in minerals than unlogged forest *consumed* soils. These inconsistent patterns could be due to food item mineral availability differing in logged verses unlogged forests. However, diademed sifakas living in fragmented and contiguous forests exhibited no difference in absolute mineral intake despite differences in overall dry matter intake (Irwin et al., 2017).

While it is possible that sifakas are consuming soil to obtain manganese ions or some mineral for which we did not sample, several studies have found that *consumed* soil mineral bioavailability often is low (Diamond, Bishop & Gilardi, 1999; Pebsworth et al., 2013), and Madagascar's rain forest soils are generally recognized as being nutrient-poor (Johnson, 2002). While we cannot outright reject the supplementation hypothesis until the mineral content of the sifaka diet and mineral bioavailability within *consumed* soils is determined, support for this hypothesis is weak. Future research would benefit from nutritional analyses of food items consumed and their bioavailability.

4.4 | Nonadaptive hypothesis

Consistent geophagy rates over space and time and the perceived risk at geophagy sites emphasize the physiological significance of this phenomenon. Combined with the impact that habitat disturbance has had on these sifakas' feeding patterns (Arrigo-Nelson, 2005, 2006; Arrigo-Nelson & Randriamahaleo, 2006), it is very likely that sifakas living at both study sites are selecting and consuming soils to serve some adaptive purpose.

Furthermore, sifaka weight and body condition data (Glander et al., 1992; King et al., 2011) provide no support for soil as a famine food (Aufreiter, Hancock, Mahaney, Stambolic-Robb & Sanmugadas, 1997). Geophagy as a cultural tradition (Hunter & De Kleine, 1984; Johns & Duquette, 1991; Mahaney et al., 1990) or a tactile or olfactory stimulator (Hladik & Gueguen, 1974, cf. Krishnamani & Mahaney, 2000) could not be assessed with these data. However, the stereotypical nature of the geophagic events observed does suggest an instinctual basis for geophagy and supports the assertion that sifaka geophagy is an adaptive behavior.

In conclusion, geophagy need not have mutually exclusive functions and may improve animal health in multiple ways. Our data suggest that geophagy by Milne-Edwards' sifakas is driven primarily by the need to detoxify consumed seeds and/or to adjust gut pH. Soil also may supplement sifaka diets with important minerals, though this is unlikely and further tests on the bioavailability of consumed minerals should be conducted (Pebsworth et al., 2013). Conformation to the protection hypothesis is supported by the fact that geophagy rates were very similar across disturbance regimes, indicating that soils serve one or many important biological functions. Further research is needed on the sifaka diet (*e.g.*, nutrient and secondary compound consumption) and digestive system (*e.g.*, sifaka gut pH); however, our study suggests that geophagy may be important in

maintaining health and wellness, especially in areas where logging, or other forms of habitat disturbance, has been experienced.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5kt172j (Semel, Baden, Salisbury, McGee, Chapple Wright, & Arrigo-Nelson, 2019)

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.