



Geophagy in Wild Yellow-Tailed Woolly Monkeys (*Lagothrix flavicauda*) Is Brief and Rare

Vinciane Fack^{1,2,3}  · Sam Shanee^{2,4} · Régine Vercauteren Drubbel¹ · Hélène Meunier^{3,5} · Martine Vercauteren¹



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Abstract

Many primates intentionally consume earth. This geophagy has probable health benefits, such as mineral supplementation or gastrointestinal tract protection, and is likely to be an important behavior for a species' ecology, health, diet, and conservation. We investigated geophagy in the Critically Endangered yellow-tailed woolly monkey (*Lagothrix flavicauda*). We collected observational data and camera trap records over 2 years at La Esperanza study site, northern Peru. Geophagy was rare, with 67 events recorded during the study. All age/sex classes engaged in geophagy, but adult males spent significantly less time consuming earth *in situ* than adult females did. Geophagy occurred predominantly during the dry season and was a solitary behavior. The forest floor is presumably a high-risk environment for these predominantly arboreal primates and our study animals employed various strategies to minimize predation risk. These included using a single route to access and leave geophagy sites, displaying increased vigilance behaviors before and during geophagy events, and minimizing the time spent on the forest floor (mean: $15 \pm SD 9$ s). They also maximized the benefits of being on the forest floor by removing earth to consume *ex situ*. These findings provide the first steps in the systemic approach required to understand the role geophagy plays in our study species, whose almost exclusive arboreality, coupled with the increased predation risk associated with terrestriality, suggests that geophagy confers an important benefit.

Keywords Atelidae · Camera trap · Earth consumption · La Esperanza · Peru · Platyrrhini

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✉ Vinciane Fack
vinciane.fack@ulb.ac.be

Extended author information available on the last page of the article

Introduction

Geophagy is the deliberate ingestion of earth-like materials such as soil, ant or termite mounds, nests (ovenbirds), chalk, and clay (Pebsworth *et al.* 2019). It has been observed throughout the animal kingdom, in various species of birds and mammals including human and nonhuman primates (Ayotte *et al.* 2006; Brightsmith and Muñoz-Najar 2004; Klaus *et al.* 1998; Krishnamani and Mahaney 2000; Matsubayashi *et al.* 2007; Young *et al.* 2011). Its occurrence in such a wide variety of species suggests that it confers an ecological advantage on individuals (Abrahams and Parsons 1996; Krishnamani and Mahaney 2000; Pebsworth *et al.* 2019).

In nonhuman primates, geophagy has been described for both strepsirrhines and haplorrhines (Blake *et al.* 2010; Krishnamani and Mahaney 2000; Pebsworth *et al.* 2019). The number of reports of geophagy among primates has increased substantially during the past decade (Adams *et al.* 2017; Blake *et al.* 2010, 2011; De Souza *et al.* 2002; Dib *et al.* 2001; Dudley *et al.* 2012; Ferrari *et al.* 2008; Link *et al.* 2011a, b; Pebsworth *et al.* 2019). The latest review counts 287 publications, highlighting geophagy in 136 of the 496 nonhuman primate species (Pebsworth *et al.* 2019). Of these, most describe geophagy sites and earth consumption qualitatively. Frequencies are provided in only 6% of publications, age/sex classes dependent frequency of geophagy in 5%, and daily and seasonal patterns of geophagy and the duration of events in only 3% (Pebsworth *et al.* 2019).

Members of all platyrrhine families other than the Aotidae have been observed engaging in geophagy, but most published observations are for the Atelidae. Geophagy is more common at Amazonian sites, where frugivory is predominant (Ferrari *et al.* 2008). For highly arboreal atelid primates, the forest floor presents increased predation risk from wild felids and snakes, as well as humans and domesticated predators (Campbell *et al.* 2005; Di Fiore 2002; Heymann and Hartmann 1991; Link *et al.* 2011b). Primates that engage in geophagy employ strategies to minimize this risk, such as increased vigilance while on the forest floor and prior to descending to the ground, forming larger subgroups at geophagy sites, and/or selecting geophagy sites that offer decreased risk (Link *et al.* 2011b). If geophagy increases predation pressure, then the associated risks must be counterbalanced by the potential benefits to individual fitness.

Lagothrix flavicauda, one of the largest and rarest neotropical primates, is endemic to the cloud forests of northern and central Peru (Aquino *et al.* 2016; McHugh *et al.* 2019; Shanee and Shanee 2011a). These primates are arboreal and have a primarily frugivorous diet (Shanee 2014a; Shanee and Shanee 2011a, b). A study of *L. flavicauda* at our field site showed that fruit made up 46% of the diet, followed by leaves (23%), insects (19%), moss (7%), buds (3%), and flowers (2%) (Shanee 2014a). Leaf consumption increased from 20% in the wet season to 36% in the dry season (Shanee 2014a). We first observed geophagy during behavioral follows of habituated *L. flavicauda* at La Esperanza, in 2015, as part of long-term research on their behavioral ecology and conservation (Shanee 2011, 2014a; Shanee *et al.* 2007; Shanee and Shanee 2011b, 2015).

Here, we examine how *Lagothrix flavicauda* individuals manage the trade-offs between risks and benefits related to geophagy. If the monkeys perceive the ground as risky, we predicted that they would increase their vigilance behavior and minimize time spent on the ground, staying only long enough to retrieve and consume soil. To

test this, we examined individuals' behavior at the geophagy site and, when possible, prior to their descent to the forest floor. We also analyzed the access and departure routes used at each site, signs of vigilance, intragroup associations, soil retrieval, event duration, differences in geophagy between age/sex classes, spatial and temporal patterns, and frequencies, providing data that are rarely given in the primate geophagy literature.

Methods

Study Site

We collected data at La Esperanza research station (S 5°39'11.60", W 77°54'55.79") in Amazonas department, northern Peru. The site is located on the eastern slopes of the Andes at altitudes between 1800 and 2400 m. Humidity is high year-round (70–99%) with a mean monthly temperature of *ca.* 14°C (Shanee 2014a) and an annual rainfall of *ca.* 1700 mm (Shanee and Shanee 2011a). The sun rises at *ca.* 06:30 h and sets at *ca.* 18:30 h. The wet season lasts from November to April, with a drier season from May to October, although it can rain at any time of the year (Shanee and Shanee 2011b). The terrain is steep, with high ridges and deep valleys. The habitat is dominated by *Ficus* spp. trees (Shanee 2014a). Canopy height is *ca.* 15–25 m with occasional emergent trees up to 35 m (Shanee and Shanee 2011a, b). The field site encompasses *ca.* 700 ha of disturbed montane cloud forest, bounded to the east, west, and south by pastures and agricultural lands with intermittent remnant forest fragments. To the north, lower elevation forests are continuous to the Rio Marañón, *ca.* 100 km (Shanee 2014a; Shanee and Shanee 2011b).

Study Group

We collected data on one habituated group of *Lagothrix flavicauda*, studied continuously since 2007 (Shanee 2014a; Shanee and Shanee 2015; Shanee *et al.* 2007). *L. flavicauda* are diurnal and highly arboreal, live in multimale multifemale groups and show few social interactions (Shanee 2014b). The mean home range size for this species has been estimated at 147 ha (Shanee 2014a). As animals were not individually recognizable, we classified animals as one of five age/sex categories: adult male, adult female, adult female with an infant, juvenile male, juvenile female. The group consisted of 24 individuals: 4 adult males, 8 adult females, 3 adult females with infants, 4 juvenile females, and 2 juvenile males. Adult males are larger than females and have a long yellow scrotal tuft (up to 15 cm) (Mittermeier *et al.* 1975). Adult females have a prominent clitoris and a smaller genital tuft. Juveniles are smaller than adults and move independently. Infants are carried by the mother. Juveniles and infants do not have yellow fur on their tails (DeLuycker 2007).

Data Collection

We employed the recommendations for standardizing research on geophagy put forward by Pebsworth *et al.* (2019) as much as possible. We made field observations in

teams of one researcher and one local field assistant. Surveys lasted 12.5 mo, spread over three periods: February–July 2016, November 2016–January 2017, July–October 2017. We conducted behavioral follows for 10 days each month, divided between 5-day field trips carried out every other week, except in July 2016, when we conducted only one field trip. We surveyed four geophagy sites using camera traps throughout the survey period and during two additional months: February and March 2017. We carried out maintenance on all camera traps once a month (changing batteries and/or SD memory cards and adjusting camera position) on the last day of field work, to not interrupt focal follows. Data were available for all months of the year, over two years, allowing us to obtain temporal patterns of geophagy. We used a portable weather station (La Crosse Technology WS1600) at the edge of the forest to collect meteorological data every 3 h during field work days (temperature, humidity, rainfall). We collected rainfall data just outside the forest edge to avoid interference from overhanging trees.

Geophagy Sites and Earth Consumption

We inventoried nine geophagy sites during the study period, two of which we knew from previous observations. All sites were located on the forest floor, always on steep slopes formed by landslips. Sites were small cavities between tree roots, where the earth was uncovered and soft, of a reddish color, and almost devoid of leaf litter or other organic material (Fig. 1). Earth at these sites was visibly different to soils in the immediate vicinity, which were compact, black, and rich in organic matter.



Fig. 1 A juvenile female *Lagothrix flavicauda* eating earth at geophagy site 3, La Esperanza, Peru. Picture from a camera trap video recorded on May 12, 2016 at 07:46 h.

Behavioral Data

We collected behavioral data through direct observations during focal animal follows, and from camera trap footage from previously identified, and potential, geophagy sites. We defined a geophagy event as one individual descending to a geophagy site and retrieving earth. When two or more individuals practiced geophagy at the site simultaneously, we counted each event separately. We defined earth retrieval as a single instance of removal of earth using either the hand or the mouth, and a consumption bout as a single instance of biting, masticating, and ingesting by one individual eating earth *in situ*. We defined vigilance as a stationary posture, motionless except for scanning movements with the head, prior to descending to the forest floor or during a geophagy event.

For focal follows, we selected a focal animal each morning, changing the age/sex category each day to ensure even sampling between categories. We started data collection when we located the group and finished when the focal animal began resting for the night, when we were unable to continue follows because of topographical and/or meteorological constraints, or when we lost the group (Shanee and Shanee 2011b). We recorded the focal animal activity at 5-min intervals and estimated its height above the ground. We divided activities into traveling, resting, feeding, foraging, social, and other activities. We grouped height above ground into seven categories: 1–5; 6–10; 11–15; 16–20; 21–25; 26–30, and >30 m. We considered geophagy as a subcategory of feeding (e.g., earth, leaf, fruit, petiole, flower consumption) and recorded it whenever we observed it, regardless of whether or not the focal animal was involved.

We used digital camera traps (Bushnell Aggressor Low-Glow 14MP Trophy Cam HD and Bushnell 8MP Trophy Cam HD) triggered by infrared motion and heat sensors to record diurnal and nocturnal geophagy events. At the start of the study, we placed camera traps at two previously identified geophagy sites. During field work, we placed an additional two camera traps at two newly identified sites (Table I). We identified these sites either through direct observations of geophagy. We did not survey some geophagy sites in this manner due to the limited number of camera traps available. We gave priority to uninterrupted monitoring of previously identified sites.

We attached camera traps to tree trunks or low branches and synchronized them by date and time. When triggered, cameras recorded for either 60 (sites 1 and 2) or 45 s (site 4). The camera at site 3 recorded 60-s videos, except between July 10, 2017 and October 16, 2017, when it malfunctioned, and only recorded 15-s videos (Table I). We set 1-s intervals between videos. Thus, cameras always recorded complete geophagy events, as one event could be recorded on consecutive videos. Camera traps were active continuously and we encountered no storage capacity problems. While testing the cameras, we recorded 10 geophagy events outside the study periods, in May and June 2017. We included these events only in age/sex class analyses. Moreover, the camera trap at site 1 was active continuously between the first two study periods and the camera trap at site 3 was active until September 13, 2016 (Table I), without geophagy records.

Table 1 Chronology of observations of *Lagothrix flavicauda* geophagy at La Esperanza, Peru

Direct observations		Camera traps											
Site	Date	N events	Total time at site (s)	N survey periods	Video duration (s)	Start date	End date	Camera trap days (24 h)	Visit days	% days visited	N events	Total time at site (s)	Total time per site (s)
1	2015 – S. Shancee pers. com.	2			60	02/01/16	03/31/17 ^a	425	3	0.71	5	107	107
					60	07/10/17	10/26/17	108	0	0	0	0	
					60	04/15/16	07/30/16	106	0	0	0	0	
2	04/26/16	1	21	3	60	11/01/16	03/31/17	151	0	0	0	0	21
					60	07/10/17	10/26/17	108	0	0	0	0	
					60	04/15/16	09/13/16 ^b	151	16	10.6	28	390	629
3	04/13/16	1	20	4	60	11/01/16	03/31/17	151	0	0	0	0	0
					15	07/10/17	10/16/17	98	3	3.06	8	145	145
					60	10/16/17	10/26/17	10	1	10	2	74	74
4	2015 – S. Shancee pers. com.	3			45	02/01/16	07/30/16	181	2	1.1	5	64	64
					45	11/01/16	03/31/17	151	0	0	0	0	
					45	07/10/17	10/26/17	108	0	0	0	0	
5	06/21/16	2	38	/	/	/	/	/	/	/	/	/	79
					/	/	/	/	/	/	/	/	
					/	/	/	/	/	/	/	/	
6	06/09/16	1	16	/	/	/	/	/	/	/	/	/	16
					/	/	/	/	/	/	/	/	
					/	/	/	/	/	/	/	/	
7	06/28/16	1	13	/	/	/	/	/	/	/	/	/	13
					/	/	/	/	/	/	/	/	
					/	/	/	/	/	/	/	/	
8	06/09/16	1	12	/	/	/	/	/	/	/	/	/	12
					/	/	/	/	/	/	/	/	
					/	/	/	/	/	/	/	/	
9	07/11/17	1	15	/	/	/	/	/	/	/	/	/	15
					/	/	/	/	/	/	/	/	
					/	/	/	/	/	/	/	/	
Total		9	176					1748	25	1.43	48	780	956

^a The camera trap at geophagy site 1 functioned continuously between the two first study periods, i.e., in August, September, and October 2016 – without geophagy records.

^b The camera trap at geophagy site 3 functioned after the end of the first study period, until 13 September, without geophagy records.

We collected data from geophagy events, recorded by camera traps or direct observation, including: date, time, location of the site, age/sex class of the individual(s), event duration, earth consumption duration, number of consumption bouts, hand or mouth used to retrieve earth, laterality, age/sex class of any conspecific present, how the animals accessed and left the site, and any *in situ* vigilance behavior. In a small number of video events, we could not identify the sex of an adult because of its position, so we added a sixth age/sex class for camera trap surveys: adult of indeterminate sex. Direct observations allowed us to record vigilance behaviors before descending to the forest floor and behavior immediately after leaving the site. We recorded all temporal measures in seconds.

Statistical Analysis

We used nonparametric tests for analyses and conducted all analyses in R 3.4.3 version (R Core Team 2017). We set the significance level to ≤ 0.05 . In most cases, individuals from the same age/sex classes did not perform geophagy on the same day, maintaining independence of events. When more than one individual of the same age/sex class did perform geophagy on the same day, direct observations and analysis of video footage allowed individual recognition. We used Chi-square tests for independence to compare hand or mouth preferences for retrieving earth, and Kruskal–Wallis and Wilcoxon tests to compare the time spent at geophagy sites between adults and juveniles, and between males and females.

Ethical Note

We used noninvasive, observational, methods in this study; no animals were handled. The research adhered to the legal requirements of Peru. We conducted data collection under permit number 173-2016-SERFOR/DGGSPFFS. The authors declare that they have no conflict of interest.

Data Availability We will provide behavioral data sets upon reasonable request to the corresponding author.

Results

Lagothrix flavicauda individuals almost never used the lower arboreal stratum (1–5 m: 1.2% of observations), preferring heights at 6–10 m (38.4%) and 11–15 m (44.4%). In 878 h and 20 min over the 12.5 mo of focal animal follows (i.e., 10, 540 data points), we directly observed 9 geophagy events, totaling 176 s. Of these 9 events, 5 occurred during behavioral scans, meaning that 0.047% of behaviors records were geophagy. During the 15 mo of camera trap surveys, we recorded geophagy on 25 (1.4%) of 1748 camera trap days (24 h). Camera traps recorded 39 videos of 48 geophagy events, totaling 780 s (0.001%) of the total 20,976 h of daytime camera surveys (taking into account only the *ca.* 12-h period that *L. flavicauda* is active) (Table I). The 10 events

recorded outside the study period (2 in May 2017 and 8 in June 2017) totaled an additional 120 s.

Geophagy Sites and Earth Consumption

Apart from two play bouts involving juveniles, animals descended to the forest floor only during geophagy events. Once at a geophagy site, the individual retrieved earth and consumed it either *in situ* or *ex situ* (Fig. 2). During the study period, monkeys did not evenly visit the sites we surveyed (Table 1). We found significant differences in the number of times sites 1, 3, and 4 were visited (Chi-square test: $\chi^2 = 46.3$, $df = 2$, $P < 0.001$). Site 3, a hidden cavity with a smaller opening than geophagy sites 1 and 4 (Fig. 1), was used most, although we monitored it less than sites 1 and 4 (410 camera days at site 3; 533 at site 1; and 440 at site 4).

Duration and Temporal Patterns of Geophagy

The mean duration of the *in situ* behavior at geophagy sites, recorded by camera traps and through direct observation, was brief: $14.8 \pm SD 9.1$ s (range: 2–45 s). We observed geophagy only during the daytime, between 06:56 h and 17:20 h, with a higher frequency of events at 09:00–10:00 h ($N = 7$), 12:00–13:00 h ($N = 9$), and 16:00–17:00 h ($N = 12$) (Fig. 3). We observed only two geophagy events between November and March (one in December 2016 and one in January 2017) and none during either February or March (wet season) of either survey year (Fig. 4). We did not observe geophagy when it rained, and geophagy was significantly more common during the dry season than in the wet season, with camera traps recording 42 events during the dry season and only 6 in the wet season (Chi-square test: $\chi^2 = 27$, $df = 1$, $P < 0.001$). We did not include data from camera trap videos recorded outside the study period in these analyses ($N = 10$).

Behavior Before and During Geophagy

We considered all 67 geophagy events for behavioral analyses. Geophagy was a predominantly solitary behavior, and 59 events involved only 1 animal. We observed

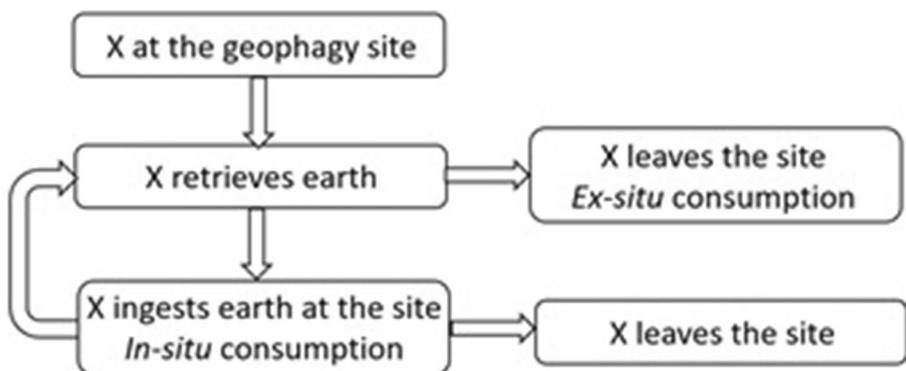


Fig. 2 Flow chart of the possibilities available to an individual at a geophagy site, at La Esperanza, Peru.

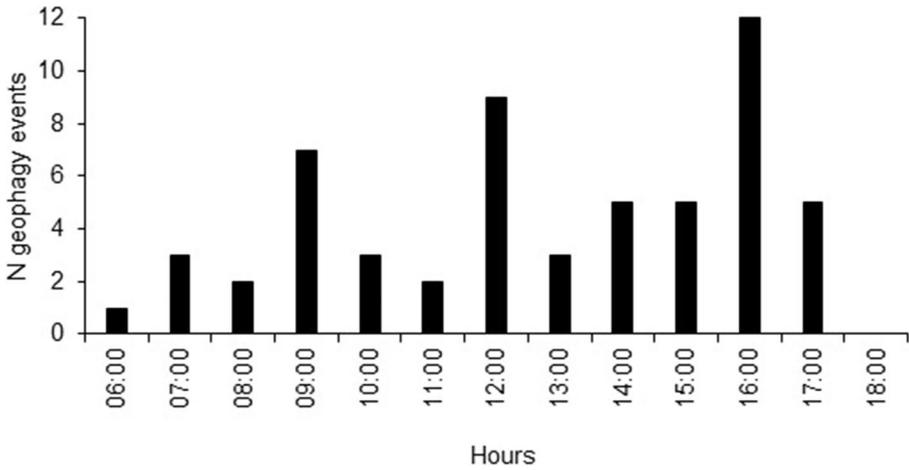


Fig. 3 Daily distribution of geophagy by *Lagothrix flavicauda* at La Esperanza, Peru, based on direct observation ($N = 9$) and camera traps ($N = 48$), 2016–2017.

pairs engaged in geophagy on four occasions, always involving a juvenile animal, and at the smallest site. We noted physical contact when the two individuals involved in the pair were both juveniles ($N = 2$), consuming earth side by side, and again when one juvenile tried to touch the other at the site, in a similar fashion to when initiating play behavior. Additionally, on four occasions, we observed one individual immediately following another to a geophagy site, and once three individuals visited the site successively, with only one animal at a time at the site. In one case, when a juvenile at the site became aware of an adult male’s presence (i.e., who was walking on a branch at 2 m from the geophagy site), the juvenile immediately left the site. We did not observe other interactions, and never saw agonistic interactions between individuals at the geophagy site.

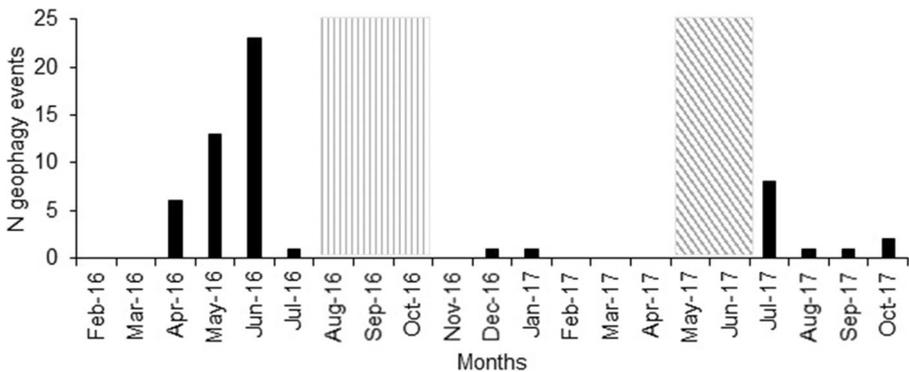


Fig. 4 Monthly distribution of geophagy events for *Lagothrix flavicauda* at La Esperanza, Peru, based on direct observation ($N = 9$) and camera traps ($N = 48$), 2016–2017. Vertical hatching represents months with two cameras functioning between the first two study periods, but without geophagy events recorded (a camera functioned continuously at geophagy site 1 and until September 13 at geophagy site 3). Diagonal hatching represents months without camera trapping but with a camera testing period (May and June 2017) during which 10 geophagy events were recorded.

Individuals accessed the ground using tree trunks. We could distinguish both the access and departure routes from the forest floor in 28 cases. In 22 of these cases (79%), individuals returned to the canopy along the same route used to access the site. Individuals showed vigilance behavior before descending to the forest floor in all our direct observations ($N = 9$). Additionally, we observed vigilance behavior on the forest floor in 30% of camera trap events.

Individuals consumed earth *in situ* (i.e., at the geophagy site) in 78% of events and also removed earth from the site before leaving in 64% of these events. When individuals descended to the geophagy site without consuming earth *in situ* (22% of events), they always removed earth from the site. When we could observe *ex situ* earth consumption, individuals always consumed it in a nearby tree ($N = 3$). The duration of a geophagy event was significantly shorter when individuals left without consuming earth *in situ* ($N = 15$, $17.2 \pm \text{SD } 9.4$ s, range: 2–45 s) than when we observed *in situ* consumption ($N = 52$, $8.1 \pm \text{SD } 6.0$ s, range: 2–31 s; Wilcoxon signed-ranks test: $Z = 11.69$, $P < 0.001$).

Age/Sex Differences

In the following analyses we included data from camera trap videos recorded outside the main study periods and excluded three records (5%) involving adults of indeterminate sex. All age/sex classes practiced geophagy, and the number of geophagy events did not differ between the sexes (Chi-square test: $\chi^2 = 0.15$, $\text{df} = 1$, $P = 0.713$) or between adults and juveniles ($\chi^2 = 0.96$, $\text{df} = 1$, $P = 0.337$) (Fig. 5). While males and females did not differ significantly in the time they spent at the site per event (males: $14.2 \pm \text{SD } 6.7$ s, females: $15.3 \pm \text{SD } 9.98$ s; Wilcoxon signed-ranks test: $Z = 465$, $P = 0.721$), males spent significantly less time consuming earth *in situ* than females (males: $2.7 \pm \text{SD } 2.4$ s, females: $7.8 \pm \text{SD } 6.6$ s; $Z = 496$, $P = 0.024$), this was also true when we only considered adults ($Z = 315$, $P = 0.006$) (Fig. 6). Adults and juveniles did not differ significantly in the amount of time spent at a site per event (adults: $14.1 \pm \text{SD } 7.8$ s,

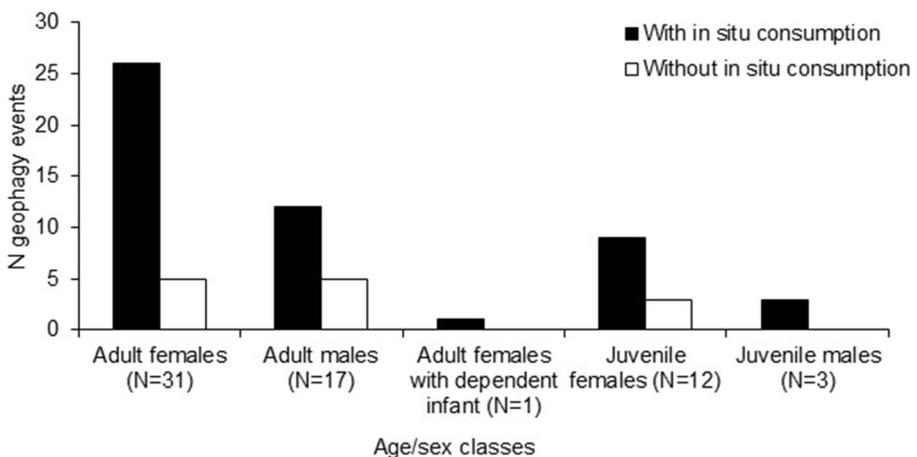


Fig. 5 Number of geophagy events by age/sex class in *Lagothrix flavicauda* at La Esperanza, Peru, 2016–2017, showing events with *in situ* consumption of earth (whether *ex situ* consumption occurred or not) and without *in situ* consumption of earth.

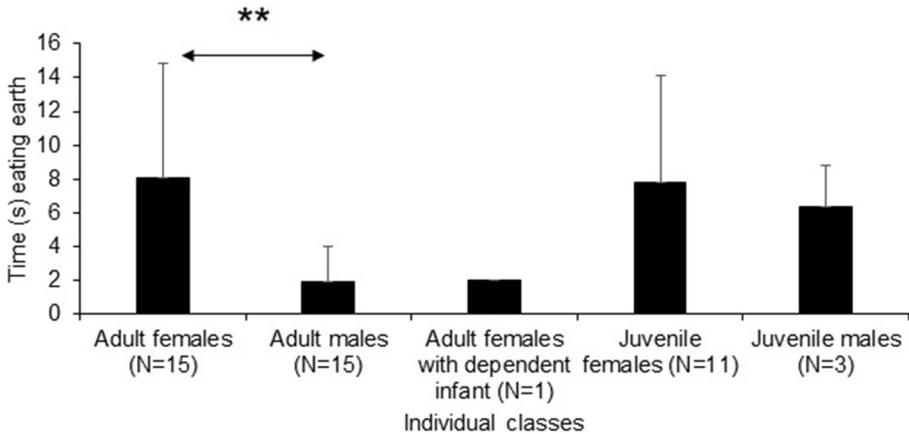


Fig. 6 Mean (\pm SD) time spent consuming earth by *Lagothrix flavicauda* at La Esperanza, Peru, 2016–2017. ** $P < 0.01$, based on a Wilcoxon signed-ranks test.

juveniles: $17.4 \pm$ SD 12.0 s; $Z = 348$, $P = 0.762$) or consuming earth *in situ* (adults: $5.8 \pm$ SD 5.4 s, juveniles: $7.5 \pm$ SD 5.6 s; $Z = 248$, $P = 0.274$). Males and females did not differ significantly in the number of bouts per event (Wilcoxon test: $W = 72$, $P = 0.071$). The most common way to consume earth *in situ* was in a single bout, although we observed females consuming earth in two, three, five, and six bouts. Juvenile males consumed earth in only one or two bouts, and adult males only ever in one bout.

The mode of earth retrieval was age dependent. Juveniles predominantly used their mouths ($N = 15$; 58%), while adults predominantly used their hands ($N = 54$; 89%) (Chi-square test: $\chi^2 = 18.18$, $df = 1$, $P < 0.001$). We observed individuals manipulating earth before consumption in 16 events (24%); 13 (81%) involving adults and 3 (19%) involving juveniles. In all but one case, individuals did these two consecutive actions with the same hand. The exception was when a juvenile used its right hand to manipulate the earth and then used its mouth to retrieve it. Similarly, individuals predominantly used the same hand for consecutive earth retrievals: adult and juvenile males did so in 100% of events, adult females in 77%, and juvenile females in 78% of events. When using hands, there was no significant difference in the hand used (right = 52%, left = 48%, $\chi^2 = 0.06$, $df = 1$, $P = 0.834$).

Adults left the geophagy site with soil in their hand or mouth more often than they left without carrying soil with them (Fig. 7, Chi-square test: $\chi^2 = 14.4$, $df = 1$, $P < 0.001$), whereas this was not the case for juveniles ($\chi^2 = 0.7$, $df = 1$, $P = 0.463$). Both males and females retrieved earth before leaving a site more often than they did not (males: $\chi^2 = 6.25$, $df = 1$, $P < 0.052$; females: $\chi^2 = 7.8$, $df = 1$, $P < 0.013$) (Fig. 7). The removal of earth before leaving the site did not affect the amount of time spent at a geophagy site (Wilcoxon test: adult: $Z = 130$, $P = 0.822$). Individuals spent $13.8 \pm$ SD 9.1 s at a site when taking earth to consume *ex situ*, and $16.3 \pm$ SD 10.4 s when leaving without taking earth.

Vigilance behaviors were unevenly distributed between age/sex classes. Juvenile males were vigilant in all geophagy events ($N = 3$); adult females during 14 of 31 events (45%); juvenile females during 4 of 12 events (33%); adult males during 5 of 17 events (29%); and adult females with infants did not show any vigilance ($N = 1$). These

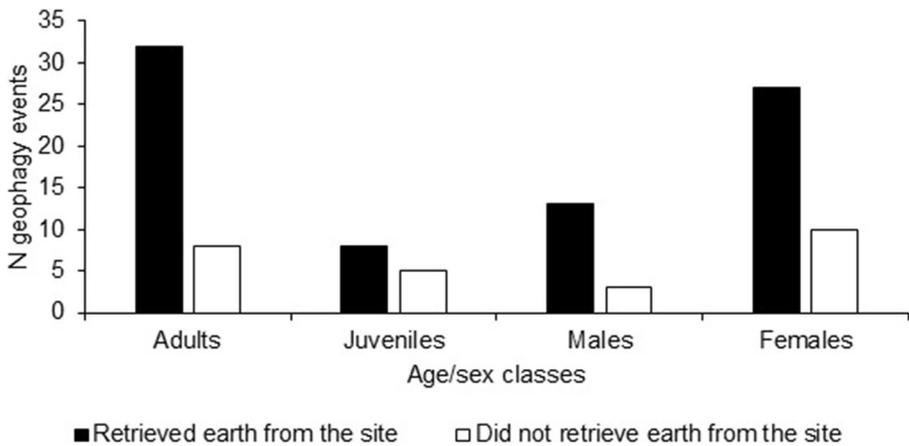


Fig. 7 *Lagothrix flavicauda* geophagy events with or without retrieving earth prior to leaving a geophagy site, at La Esperanza, Peru, 2016–2017.

differences were not significant (excluding adult females with infants, adults vs. juveniles $\chi^2 = 0.12$, $df = 1$, $P = 0.764$, females vs. males: $\chi^2 = 0.02$, $df = 1$, $P = 0.937$).

Discussion

Our results show that geophagy in *Lagothrix flavicauda* is a rare, but seemingly important, behavior. Our study animals risked descending to the forest floor, almost exclusively for geophagy, spending the vast majority of their time >5 m above the ground. Predators of this species found at the study site include pumas (*Felis concolor*), ocelots (*Leopardus pardalis*), and margays (*Leopardus wiedii*) (Shanee and Shanee 2018), but by far the greatest potential predatory pressure at the site comes from humans and domestic dogs. Additionally, the forest floor is a resource-poor stratum for primates in neotropical forests (Di Fiore 2002). This may help explain the low incidence of terrestriality we observed in *L. flavicauda*, as in the majority of neotropical primates (Campbell *et al.* 2005; Di Fiore 2002). Geophagy appears to be important enough that all age/sex classes risk descending to the ground, suggesting that this behavior is crucial to their fitness. The obvious vigilance, and removal of earth for *ex situ* consumption, reduces risk and increases benefits of exposure to the risks of terrestriality for geophagy.

Geophagy was not observed in *Lagothrix flavicauda* for the first 8 years of studies at La Esperanza (S. Shanee *pers. obs.*), probably due to a combination of the rarity of the behavior, the difficult field conditions, and the perceived risk involved in individuals that are not fully habituated to researcher presence, as observed in studies of the titi monkeys where study duration (as a proxy measure of habituation) was positively correlated with observations of terrestrial activity (Souza-Alves *et al.* 2019). It is also difficult to observe such a brief behavior, especially if the focal animal is not involved. Camera traps provide an excellent tool for the study of such elusive behaviors, and geophagy was one of the first applications of this technology (Pebsworth *et al.* 2012; Pebsworth and LaFleur 2014). The use of camera traps should be considered as a

preferred method to study geophagy if sites are revisited by monkeys, as it can record continuous, detailed behavioral data, at many sites simultaneously, with comparatively little effort.

We observed geophagy throughout the day, except after 18:00 h. We recorded more events during the 9:00–10:00, 12:00–13:00, and 16:00–17:00 h slots. Very few studies have documented daily patterns of geophagy in primates (Pebsworth *et al.* 2019). The reason for temporal differences in geophagy expression is unknown, but some hypotheses have been formulated linking these patterns to predator avoidance, movement of the animals, and/or feeding behavior (Blake *et al.* 2010).

In primate geophagy, the most commonly consumed earth types come from the forest floor and terrestrial or arboreal termitaries (Pebsworth *et al.* 2019). *Lagothrix flavicauda* consumed earth defined as “base of uprooted trees or under bole of a tree” (Pebsworth *et al.* 2019, p. 180), a fairly uncommon source for geophagy, representing only 8% of nonhuman primate geophagy records. It seems that they specifically selected geophagy sites based on some visible characteristics (slope, landslide, soil color, fallen tree, lianas). Moreover, our study animals preferred certain sites, possibly due to safer access and lower predation risk. Easier access, and the availability of “escape” routes, may also play a role in site selection. For instance, *Alouatta seniculus* and *Ateles belzebuth* select geophagy sites according to predation risk in the area (Izawa 1993; Link *et al.* 2011b). Preferred sites may also be richer in clay or other minerals lacking in the animals’ diets. Alternatively, preferred sites may have a “better” location in relation to group travel routes, and the presence of other food resources in the vicinity. However, this seems less likely in the case of site 3, the most preferred site, as there were several other geophagy sites in the immediate vicinity that the monkeys visited much less frequently.

In the case of *Lagothrix flavicauda*, geophagy was a predominantly solitary behavior, unlike in other Atelines, such as *Brachyteles arachnoides hypoxanthus*, *Ateles hybridus*, *Ateles belzebuth*, *Alouatta seniculus*, and *Alouatta belzebul* (De Souza *et al.* 2002; Dib *et al.* 2001; Link *et al.* 2011a, b), among which geophagy is practiced in a group. The solitary nature of geophagy in *L. flavicauda* may reflect their overall lower level of sociality, or it could simply be due to the small size of the geophagy sites, limiting access to one individual at a time. The surface areas of two of four sites used by *A. belzebuth* and *A. seniculus* in Colombia were 200 and 400 m² (Link *et al.* 2011b), allowing many more individuals to perform geophagy simultaneously.

Geophagy in *Lagothrix flavicauda* was seasonal, observed almost exclusively during the dry season. This suggests that it may not be to treat potential parasitic infections, which are generally more common in the wet season (Huffman *et al.* 1997). Only three publications have shown increased geophagy during the wet season, when toxin consumption may be lower but potential parasitic infection higher (Dib *et al.* 2001; Hsu *et al.* 2001; Setz *et al.* 1999) and geophagy may act as an anti-diarrheal (Knezevich 1998). Eight studies reported increased geophagy during the dry season (Pebsworth *et al.* 2019). Of these, five were conducted on neotropical primates (Blake *et al.* 2010; De Souza *et al.* 2002; Heymann and Hartmann 1991; Müller *et al.* 1997; Veiga and Ferrari 2007). These findings support the hypothesis that geophagy acts as a form of self-medication against secondary compounds produced by plants, if the diet also changes with season (Hladik 1977; Mahaney *et al.* 1995). However, seasonality of

geophagy may also support the supplementation hypothesis where earth consumed provides micronutrients absent in usual dietary components (Eudey 1978).

Individuals from all age/sex classes performed geophagy a similar number of times, although they rarely engaged in this behavior together, suggesting that all animals derived some benefit from geophagy. However, age/sex classes did differ in the amount of time spent eating earth *in situ* and in the number of bouts per event, with adult males spending much less time eating and fewer bouts. This could be related to adult males' role in group defense, that could not be assured while on the forest floor. As we did not recognize males individually, oversampling of the alpha male, who may play an important role in group defense (Snyder-Mackler *et al.* 2012), may have skewed our results.

We observed interesting differences in the mode in which animals retrieved earth. Adults used their hands, while younger animals mainly retrieved earth directly with their mouths. The earth at the geophagy sites was very soft, suggesting that this is not because juveniles are too weak to retrieve heavily compacted soil. Adults also removed earth to consume *ex situ* more often than juveniles did. If geophagy is a learned behavior we would expect younger animals to use different, simpler, techniques than older group members, whose technique would improve with experience. Juveniles may also be more naïve than adults about the risks linked to terrestriality. Using the mouth to retrieve earth reduces vigilance at the moment of the retrieval. Conversely, adults could monitor the surroundings while retrieving earth with their hands. Juveniles were also less likely to retrieve earth prior to leaving geophagy sites, thus reducing the benefits of visiting the site. Interestingly, we never observed young animals practicing geophagy together with adult males.

Adults showed no difference in hand use when retrieving earth, although we could not examine individual hand use preference. Individuals generally used the same hand for successive actions. This may be due to individual preference, or to postural constraints related to the size and shape of the sites, with individuals using one hand for support and the other for soil retrieval (Macneilage *et al.* 1987). For instance, chimpanzee posture while ant-fishing influenced manual laterality (Marchant and McGrew 2007). Nevertheless, retrieving earth might not be a complex enough task to highlight manual laterality in our group. No particular ability or precision is needed to reach food items, which represents a low-level task that cannot reveal hand preference in nonhuman primates, unlike high-level tasks requiring, for instance, precise spatial positioning (Fagot and Vaclair 1991).

Despite growing interest in geophagy in nonhuman primates, very few studies have provided detailed descriptions of geophagy-linked behaviors (Pebsworth *et al.* 2019). We have taken the first steps in the systemic approach required to build our understanding of the role geophagy plays in nonhuman primate ecology. For example, we need to examine the relationship between the chemical composition of consumed earth and dietary items and the temporal pattern of geophagy. It is still unclear why *Lagothrix flavicauda* practices geophagy, but their almost exclusive arboreality, coupled with the increased predation risk associated with terrestriality, suggests that geophagy confers an important benefit.

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Affiliations

Vinciane Fack^{1,2,3} · Sam Shanee^{2,4} · Régine Vercauteren Drubbel¹ · Hélène Meunier^{3,5} · Martine Vercauteren¹

¹ Faculté des Sciences, Service d'Anthropologie et Génétique humaine CP.192, Université libre de Bruxelles, Brussels, Belgium

² Asociacion Neotropical Primate Conservation Peru, La Esperanza, Yambrasbamba, Amazonas, Peru

³ Centre de Primatologie de l'Université de Strasbourg, Strasbourg, France

⁴ Neotropical Primate Conservation, Seaton, Cornwall, UK

⁵ Laboratoire de Neurosciences Cognitives et Adaptatives, UMR 7364, CNRS et Université de Strasbourg, Strasbourg, France