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ORIGINAL ARTICLE

Geophagy in large-headed capuchin monkeys (*Sapajus apella macrocephalus*) in the Reserva Nacional Tambopata, Peru

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Abstract

Many primate species have been observed descending to the forest floor to intentionally consume soil (geophagy) at licks. The practice of geophagy is assumed to provide health benefits, such as mineral supplementation and/or gastrointestinal tract protection. We collected data on geophagy events through the use of camera traps at Tambopata National Reserve in southeastern Peru. Two geophagy sites were monitored for 42 months, during which time we observed repeated geophagy events by a group of large-headed capuchin monkeys (*Sapajus apella macrocephalus*). To the best of our knowledge, this is the first report of its kind for the species. Geophagy was rare, with only 13 events recorded over the study period. All but one event took place during the dry season, and 85% of events took place in the late afternoon between 1600 and 1800 hours. The monkeys were observed consuming soil both in situ and ex situ, and displayed heightened vigilance behavior during geophagy events. Although the small sample size makes it difficult to draw clear conclusions as to the drivers of this behavior, the seasonal timing of the events and the high percentage of clay in the consumed soils suggest that these events are linked to the detoxification of secondary plant compounds in the monkeys' diet.

Keywords Clay lick · Mineral lick · Soil consumption · Terrestriality

Introduction

Geophagy is the intentional ingestion of soil and soil-like materials (Krishnamani and Mahaney 2000). This often takes place at sites referred to as a clay lick or mineral lick. These are specific sites with exposed soil containing relatively high percentages of clay and/or certain minerals (Brightsmith and Munoz-Najar 2004; Emmons and Starck 1979). Research suggests that there are several non-exclusive benefits to geophagy depending on the diet, age, sex and reproductive state of the species involved and ecological conditions (Krishnamani and Mahaney 2000; Pebsworth et al. 2019a, b). The two main hypotheses suggest that animals ingest earth for detoxification purposes and/or to supplement their diet with minerals which are not easily available to them from other food sources (Gilardi et al. 1999; Johns and Duquette 1991; Pebsworth et al. 2019a, b). The difficulty in obtaining these minerals from plant materials may explain why geophagy is common in frugivores and folivores (Kreulen 1985).

The importance of geophagy to some arboreal species is such that they will descend to the forest floor in order to access geophagy sites, potentially exposing themselves to greater predation risk from terrestrial animals (Bello et al. 2022; Griffiths et al. 2020; Link et al. 2011). Despite the risk of predation, many primate species frequently engage in geophagy (Pebsworth et al. 2019a; 2019b), suggesting that the benefits outweigh the potential risks associated with terrestriality, even for arboreal primates.

Geophagy has been observed in 136 non-human primate species, which belong to about half (39) of all primate genera (Pebsworth et al. 2019a; 2019b). However, very few records exist for capuchin monkeys. Tufted capuchins (*Sapajus apella*; *Cebus apella* in original references) in Colombia have been observed consuming soil from arboreal termite mounds (Gomez 2003), but we found no clear reports of wild *Cebus* or *Sapajus* populations engaging in

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terrestrial geophagy. However, terrestrial geophagy has been documented for other large Neotropical primates, such as *Alouatta*, *Ateles* and *Lagothrix* (Blake et al. 2010; Fack et al. 2020b, a; Link et al. 2011). In a review of geophagy in New World monkeys, Ferrari and Urbani (2008, referring to Baker 1999) report geophagy in *Cebus capucinus* in Costa Rica. However, it was not specified as to whether the consumed soil originated from a clay lick or an arboreal termite mound (Pebsworth et al. 2019a, 2019b). Urbani (2004), though, did report geophagy and earthworm consumption in *Cebus olivaceus* on an artificial island at a zoological facility in Caracas.

Here we provide, to the best of our knowledge, the first unambiguous report of terrestrial geophagy in large-headed capuchin monkeys (*Sapajus apella macrocephalus*), which were observed in the Tambopata National Reserve, Peru.

Methods

Kawsay Biological Station was used as a base camp to enter the study area (Fig. 1). Terrestrial geophagy sites were monitored in the Briollo and Sandoval sectors of Tambopata National Reserve, Madre de Dios, Peru (12°32′S, 69°00′W). These sites were selected based on their accessibility and their high densities of animal footprints. The forest in the area is seasonally flooded primary subtropical wet forest (Holdridge 1967). The area has two distinct seasons, a dry season that runs from May to October and a wet season that runs from November to April. The historical average annual rainfall in the area is 2297 mm, and fluctuates strongly between seasons, with ~ 30 mm of rainfall in the driest month and ~ 400 mm in the wettest month. The average annual temperature is 31.3 °C, with the highest temperatures recorded in September and the lowest in May [Servicio Nacional de Meteorología e Hidrología (SENAMHI) 2016].

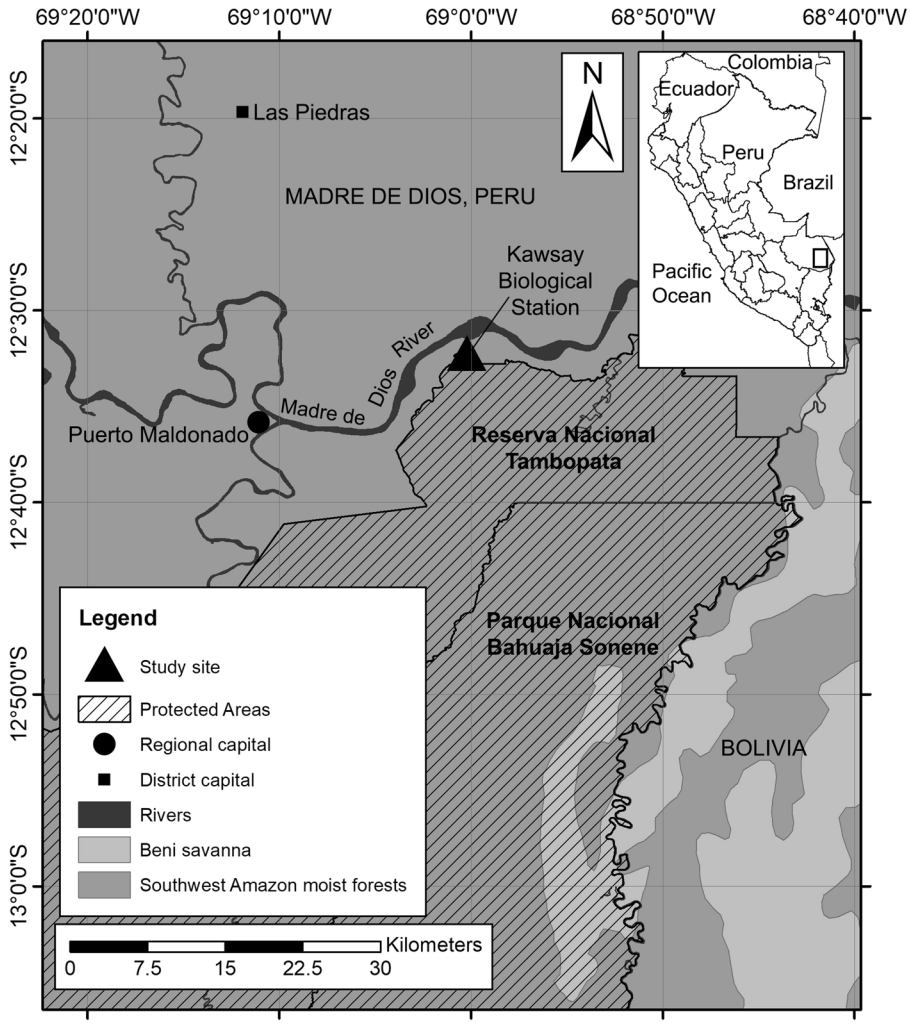

Fig. 1 Map of the field site, including ecoregions and nearby protected areas (Dinerstein et al. 2017)

Camera traps (Trophy HD Aggressor; Bushnell, Overland Park, KS) were installed at two different terrestrial geophagy sites (Collpa Altura and Collpa Grande). The sites are ~ 900 m apart. Each camera was placed 30 cm above the ground at a slightly downward angle to ensure the videos captured the whole site. The monitored geophagy sites were in the forest interior (Montenegro 2004), situated in primary forest near to *aguajales*, which are swamps dominated by aguaje palms (*Mauritia flexuosa*). Triggered camera traps recorded for 10 s, with an interval of 3 s between videos. Camera traps were checked every 2 weeks, at which time we changed the memory cards and batteries if necessary. The survey ran for 42 months, between April 2018 and September 2021. Videos from the camera traps were reviewed for geophagy events involving primates. Independent geophagy events were defined as an individual or a group retrieving soil at a different clay lick, or at the same clay lick after a 30-min interval between videos.

Soils were sampled from the cavities of the licks where the capuchin monkeys were observed engaging in geophagy. Additionally, control soils were also sampled from the forest floor 2 m away from the licks. The samples were collected by hand and latex gloves were worn during sampling; the gloves were changed between each sample. We collected approximately 500 g of soil in clean Ziploc bags for each sample. The bags were then sealed and tagged in situ, after expelling the air. At the base camp, the bags were stored together in a larger bag in a dark and dry environment. Soil samples were sent to the Laboratorio de Analisis de Suelos, Plantas, Aguas y Fertilizantes (Universidad Nacional Agraria La Molina, Lima) 5 days after collection.

Ethical note

This research adhered to all the relevant laws of Peru and was conducted under a tripartite agreement of institutional cooperation between Kawsay Biological Station, Tambopata National Reserve and the Asociación para la Investigación y Desarrollo Integral. The research protocols followed the American Society of Primatologists' Principles for the Ethical Treatment of Non-human Primates.

Results

The final sampling effort consisted of 1164 trap-days (754 and 410 trap-days at each clay lick, respectively). Thirteen geophagy events involving *Sapajus apella macrocephalus* were recorded; the trap rate was 11.2 [calculated according to the formula (no. of events/no. of trap-nights) × 1000 (Tobler et al. 2008)]. We were not able to confidently determine the sex of individuals from the videos. All but one of the events occurred at the same clay lick (Collpa Altura). Geophagy predominantly occurred in pairs or groups of three individuals; only two events were recorded for a solitary individual, and only one event was recorded for a group larger than three, which comprised six individuals (Table 1). Geophagy event duration was highly variable, with a minimum of 10 s and a maximum of 24 min 27 s (mean, 7 min 47 s; median, 5 min).

All the events but one occurred during the dry season. The events were not evenly distributed across the study period, with ten of the 13 events occurring in 2021. Eleven events (85%) occurred between 1600 and 1736 hours, and the other two events occurred between 1430 and 1600 hours.

Table 1 Overview of the recorded geophagy events in capuchin monkeys during the study [start and end times refer to the arrival of the first individual at the site (first video) and the departure of the last individual, respectively]

Event ID	Date	No. of individuals during event	Time[a] (start)	Time[a] (end)	Duration[b]	Clay lick ID
1	26 October 2019	2	17:01:32	17:08:04	00:06:32	Altura
2	29 October 2019	2	17:10:59	17:11:09	00:00:10	Altura
3	28February 2020	1	17:18:19	17:26:53	00:08:34	Altura
4	25 July 2021	6	16:23:45	16:48:12	00:24:27	Altura
5	26 July 2021	3	17:32:32	17:36:30	00:03:58	Altura
6	3 September 2021	2	16:29:22	16:33:10	00:03:48	Altura
7	5 September 2021	2	16:42:04	17:00:49	00:18:45	Altura
8	17 September 2021	3	15:47:28	15:50:58	00:03:30	Altura
9	17 September 2021	2	17:18:23	17:23:23	00:05:00	Altura
10	19 September 2021	2	14:53:04	15:01:27	00:08:23	Altura
11	20 September 2021	1	17:26:25	17:27:10	00:00:45	Altura
12	21 September 2021	2	17:06:06	17:21:43	00:15:37	Altura
13	23 September 2021	2	17:16:32	17:18:12	00:01:40	Grande

ID Identifier

[a, b] Time and duration are presented as hours:minutes:seconds

Fig. 2 **a** A capuchin monkey consumes soil while a squirrel monkey forages in the background. **b** Two individuals manipulate soil from the clay lick while another individual remains vigilant

During one event squirrel monkeys (*Saimiri boliviensis*) foraged together with the capuchin monkeys (Fig. 2a), but the former were not observed to consume soil.

Individuals in the observed events manipulated large chunks of soil that they broke into smaller pieces, which were then consumed either in situ or ex situ. During these events monkeys showed heightened levels of vigilance, defined as being motionless except for scanning movements of the head. In all observations the monkeys were vigilant before descending to the forest floor, and in 39% of events they performed vigilant behaviors while on the forest floor. In one video an individual stands on its hind legs, visually scanning the surrounding area while the rest of the group manipulate soil (Fig. 2b). Individuals consumed earth in situ in 46% of events, and in all events removed earth from the site for ex situ consumption. When we were able to observe ex situ soil consumption, the soil was consumed by individuals in a nearby tree. When geophagy was performed by a solitary individual ($n = 2$), the soil was exclusively consumed ex situ.

During the study period, we also recorded 11 geophagy events for *Ateles chamek* and 33 for *Alouatta sara.* All but one geophagy event recorded for *A. chamek* took place at Collpa Grande, and all the events were registered during the dry seasons of 2018 and 2021. For *A. sara*, we recorded 14 events in Collpa Grande and 19 in Collpa Altura. Fifteen of these events were registered during the dry seasons of 2018, 2019, 2020 and 2021, and 18 during the wet season of 2020.

The soil of the licks was identified by analysis as silty clay, while the control samples were identified as loamy soils. The licks contained higher percentages of clay and lower percentages of sand than the control samples. No clear differences were found in the minerals present in the soils, except for much lower levels of potassium in the samples collected from the licks. Full results of the analyses are given as supplemental material. We did not conduct any statistical analyses due to the small sample size.

Discussion

Ferrari and Urbani (2008) argued that the absence of any clear reports of geophagy in wild capuchin monkeys was due to a lack of studies rather than the absence of this behavior. However, capuchins are generally better studied in the wild than many other Neotropical primates for which geophagy has been observed (e.g. Fack et al. 2020b, a; Hawes et al. 2013). The lack of observations of geophagy in capuchin monkeys may therefore be due to its rarity in their behavioral repertoire. Similarly, geophagy has been shown to be a rare behavior in other primate species (Fack et al. 2020b, a; Mahaney et al. 1995; Setz et al. 1999; de Souza et al. 2002).

Capuchins are known for their destructive foraging technique when searching for invertebrate prey (mainly hymenopterans and isopterans), and as many of these prey species incorporate soil into their nests, the capuchins may accidentally ingest small amounts of soil and related substances during this activity (Ferrari and Urbani 2008). Geophagy has been confirmed where capuchin monkeys have been reported to feed on the soil of termite mounds (Gomez 2003); however, soil from termitaria usually has a different composition, including that of minerals, to surface soil (de Souza et al. 2002). This could explain why we observed several soil consumption events in the present study regardless of the increased predation risk to these arboreal primates when they come to the ground, but no consumption of termitaria despite the vast number of arboreal termitaria available at the study site. Consumption of arboreal termitaria by *Ateles chamek* has been observed occasionally at the field site (S. Pottie and R. Bello, personal observation), and both *A.*

chamek and *Alouatta sara* have been observed consuming soil exclusively in situ from clay licks at our site.

The fact that all the events occurred during the afternoon, and predominantly in the hours before sunset, is contrary to observations on *Ateles* and *Alouatta*, which most frequently visit clay licks just after midday (Link et al. 2011). A study of *Lagothrix flavicauda* showed higher numbers of geophagy events between 1600 and 1700 hours, although geophagy also took place throughout the day (Fack et al. 2020b, a). These temporal differences in geophagy may be linked to site- and species-specific factors related to predator avoidance, movement of the animals, and/or feeding behavior (Blake et al. 2010).

The capuchin monkeys were most commonly observed engaging in geophagy in pairs or groups of three. This contrasts with most other large platyrrhine species, for whom geophagy has been observed to be either a predominantly solitary behavior, as found in *L. flavicauda* (Fack et al. 2020b, a), or a group behavior, as found in *Ateles* (Link et al. 2011). This difference may be explained by the smaller group sizes of *S. macrocephalus* (when compared to *Ateles*), combined with their higher level of sociality (as compared to *L. flavicauda*) (Fragaszy et al. 2004). The average duration of events in our study was longer than those reported for other Neotropical primate species (de Souza et al. 2002; Fack et al. 2020b, a), with the exception of species of the genus *Ateles* (Link et al. 2011). It is possible that capuchins are more accustomed to foraging and manipulating foods on the ground than other predominantly arboreal primate species, and therefore remain on the forest floor for longer (Lopes-Palmeira and Camara-Pianca 2012; Reitsema et al. 2020; Soley et al. 2017).

Due to the rarity of geophagy and the small sample size (only two clay licks were monitored, although there are probably more in the area), our results are preliminary and we have to interpret them with caution. However, the predominance of geophagy during the dry season could indicate a causal relationship with diet, due to either seasonal scarcity of some nutritional resource or seasonal variation in the intake of secondary plant compounds (Baker 1999; Conceição Medeiros et al. 2021; Dawson 1976; Holdo et al. 2002; de Souza et al. 2002; van Schaik et al. 1993; Veiga and Ferrari 2007). The relatively high percentage of animal material in the diet of capuchin monkeys (Gómez-Posada 2012) may reduce their need for mineral supplementation through geophagy. The results of the soil analysis also appeared to confirm this, as no clear differences in mineral composition were found between the soils from the licks and the control samples, except for lower levels of potassium in the former, a mineral that has not been mentioned in the literature as of relevance for geophagy.

Soil ingested through geophagy has been found to play an important role in the detoxification of certain secondary plant compounds, such as tannins and alkaloids, during the dry season (Gilardi et al. 1999; Mahaney et al. 1995). Greater consumption of these compounds in the dry season has been shown to be a result of a change in diet during this period because temporal scarcity of other food resources often leads to the incorporation of a higher proportion of leaves and seeds into the diet of non-human primates (Fack et al. 2020b, a; Mahaney et al. 1995; de Souza et al. 2002; Terborgh 1983). Clay-rich soils have been shown to neutralize some of the tannins and alkaloids in the digestive tract of non-human primates (Gilardi et al 1999; Gurian et al. 1992). The fact that there were much higher percentages of clay in the soils from the licks than in the control samples appears to support this hypothesis. Furthermore, fruit availability is lowest between July and September at our study site (Medina et al. 2011). The effect of this on the diet of the local capuchin population has not been studied, but groups of *A. chamek* at the study site were shown to incorporate a higher percentage of leaves into their diet during these months (Bello 2018). It was also observed that *A. chamek* utilized clay licks at the study site only during the dry season. Geophagy in the howler monkeys at the study site appeared to be less affected by seasonality, with only 15 of the 33 events observed in this species taking place during dry seasons. This might be related to their more folivorous diet (Strier 1992), as this may mean that they need to detoxify secondary plant compounds throughout the year. This in turn suggests that the seasonal bias of geophagy in the population of capuchin monkeys during the dry season may be related to the detoxification of certain tannins and alkaloids.

Although geophagy events involving capuchin monkeys were mainly recorded during the dry season, it is important to note that eight of the 13 events took place over one month, September 2021. A possible explanation for this is the temporally dynamic nature of mineral licks, which are resources that appear and disappear over time (Griffiths et al. 2022). It is also possible that the capuchins used unmonitored clay licks, which may have dried up towards the end of the 2020 dry season. Alternatively, they may rotate between several different clay licks over a certain period of time, and/or it is possible that changes in climatic variables between years could influence their diet and therefore their need to consume soil.

Despite recent advances, still relatively little is known about geophagy in most primates (Pebsworth et al. 2019a, 2019b), and this behavior, to the best of our knowledge, has not previously been conclusively documented for large-headed capuchin monkeys in the wild. Given the rarity of geophagy, and the difficulties associated with long-term observational studies, it is very possible that further research may show geophagy to be present in many other species of capuchin monkeys.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10329-023-01058-9.

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Data availability Data are available from the table, figures and supplementary material.

Declarations

Conflict of interest Not applicable.

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