

# Geophagy by Sanje Mangabeys (*Cercocebus sanjei*) of the Udzungwa Mountains, Tanzania: Patterns of Soil Consumption in a Highly Frugivorous Primate

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**Abstract:** Geophagy, defined as the deliberate consumption of soil, has been observed in several primate species. However, its aetiology and function(s) remain poorly understood. The major adaptive hypotheses for the role of geophagy are “protective” to alleviate gastrointestinal distress due to the consumption of plants, parasites and/or pathogens, or a source for “dietary supplementation.” In this study, we investigated patterns and potential drivers of soil consumption in the Sanje mangabey, an endemic monkey from Tanzania, by analysing the events of geophagy in relation to temporal and dietary variation. We found that the mangabeys consumed significantly more soil during periods of high ripe fruit availability (November to May; GLM:  $F = -0.00175$ ,  $df = 33$ ,  $p = 0.032$ ). Conversely, unripe fruit availability did not impact the occurrence of geophagy (GLM:  $F = 0.000158$ ,  $df = 33$ ,  $p = 0.225$ ); however, unripe fruit made up only 1% of the annual diet, whereas, ripe fruit comprised the majority of the annual diet from 71 to 85%. Rainfall and elevation of soil sites did not impact geophagic behaviour. Highly frugivorous diets are characterised by high soluble carbohydrate concentrations and low fibre. A combination of high fructose diets and reduced polysaccharides has been associated with gastrointestinal (GI) distress in human-provisioned groups of primates; hence, the results of this study suggest that geophagy in the Sanje mangabeys may function in relieving dietary GI distress.

**Key words:** soil consumption, mangabeys, GI distress, frugivorous

## INTRODUCTION

Geophagy, the deliberate consumption of soil (Nishihara & Kuroda 1991), is observed in 136 species and subspecies of extant primates (Pebsworth *et al.* 2019). Since 2000, 97 new species and subspecies of primates have been described; thus, it is likely the number of geophagic taxa is much higher in reality (Davies & Baillie 1988; Krishnamani & Mahaney 2000; Pebsworth *et al.* 2019). This behaviour is also reported in elephants (African elephants, *Loxodonta africana*, Weir 1969); ungulates (mule deer, *Odocoileus hemionus*, Arthur & Alldredge 1979; domestic cattle, Mahaney *et*

*al.* 1996); birds (Diamond *et al.* 1999) and reptiles (Kreulen & Jager 1984); however, its aetiology remains poorly understood (Young *et al.* 2012).

The benefits of geophagy can be dependent on dietary type, anatomy, and taxonomy (Young 2011). One of the most parsimonious hypotheses argues that soil consumption functions to adsorb toxins. Some soils, expressly clays that aid in adsorption (Jones 1957; Daykin 1960), may be able to adsorb plant secondary metabolites (PSMs, e.g., phenolics, tannins, Ta *et al.* 2018). Such soils, once ingested, can minimise the PSM's inhibition of protein uptake

(Gurian *et al.* 1992). However, the concentration of these toxic metabolites is not equally distributed throughout the plant, with mature leaves typically containing three times (up to 200 – 500 millimolar/mM) the amount of PSMs compared with fruit, but depends on leaf maturity and environmental factors (Salminen & Karonen 2011). Thus, if geophagy functions to mitigate against toxins, it should be found among highly folivorous species and be less common among highly frugivorous species whose diets consist of fewer plant secondary compounds (Glander 1982; Mowry *et al.* 1996). Janzen (1975) suggested plants growing in nutrient-poor soils, such as tropical rainforests, produce higher concentrations of defensive secondary compounds compared with their temperate counterparts. These metabolites are likely to be related to duration of the dry season and developmental stage of the plant (Ramakrishna & Ravishankar 2011). Hence, mature plants in tropical forests with a prolonged seasonal dry period contain greater concentrations of secondary plant compounds. Low-water input causes oxidative stress in plants, resulting in increases in flavonoids and phenolic acids (Larson 1988), suggesting that animals feeding on such plants should practice geophagy at higher frequencies during periods of drought stress. However, dietary variation associated with plant phenology and availability of young leaves and ripe fruit (van Schaik *et al.* 1993) may impact the intake of these toxic chemicals. Thus, primates may reduce their intake by consuming food items with a lower concentration of toxins (e.g., ripe fruit and animal matter), bypassing the need for soil absorption.

Relieving gastrointestinal (GI) distress has been suggested as one function of geophagy. For example, Goltenboth (1976) found that anaerobic fermentation of mature leaves within the fore-stomachs of leaf monkeys led to increased concentrations of volatile fatty acids, subsequently decreasing the pH and causing fatal “acidosis” (supported by Davies & Baillie 1988). In such cases, ingesting clay minerals may buffer against these volatile fatty acids, adjusting pH to a normal level. Alternatively, geophagy may function as an antidiarrhoeal agent, with Mahaney *et al.* (1995) witnessing seasonal geophagy corresponding with the dry season amongst mountain gorillas. In this species, it was suggested to be an antidiarrhoeal strategy to combat sudden dietary shifts from leafy plants to diets dominated by bamboo shoots (*Arundinaria alpine*). Similarly, in human medicine, clay minerals such as halloysite, metahalloysite, and kaolinite are active agents in traditional and pharmaceutical antidiarrhoeal remedies. For example, Kaopectate (Pharmacia &

Upjohn, Peapack, New Jersey, U.S.A) and Smecta Diosmectite, a natural silicate of aluminium and magnesium, are used to treat acute diarrhoea (see Young *et al.* 2011; Khediri *et al.* 2011).

Our objective here is to provide the first detailed report of geophagy by the Sanje mangabey (*Cercocebus sanjei*), endemic to the Udzungwa Mountains of Tanzania (Ehardt *et al.* 2005; McCabe *et al.* 2019). Geophagy has been observed in the Sanje mangabey (Figure 1); however, its pattern of occurrence has not been described and its function in this species is not yet clear. Here we describe the pattern of soil consumption with respect to seasonal fruit availability, elevation of consumption sites and seasonal rainfall. Food availability for the mangabeys is influenced by rainfall, with higher fruit availability occurring in the wet season compared to the dry season (McCabe *et al.* 2013). The mangabeys are monogastric omnivores, feeding on fruits, seeds, flowers, roots, fungi, and invertebrates; however, fruit (i.e., whole fruits with seeds and fruit pulp) comprises the largest proportion of the annual diet (71 to 85%, McCabe *et al.* 2013). To attempt to separate the protective and GI distress hypothesis we tested contradictory predictions: (1) soil consumption will occur more frequently during low rainfall, resulting in increases in secondary plant metabolites and associated protective function and, conversely, (2) mangabeys will display increased soil consumption with higher fruit availability owing to the low fibre, high fruit diet and associated GI distress.

## METHODS

### Study Site and Subjects

The Udzungwa Mountains of Tanzania are rich in biodiversity, and a part of the Eastern Afromontane Biodiversity Hotspot (Mittermeier *et al.* 2004). This is a network of 25 biogeographic areas accounting for only 1.4% of the world’s land mass, yet it contains 62% of vascular plants and non-fish vertebrate biodiversity with a high level of endemism; e.g., ca. 30% of the 2000 moist tree plants are endemic to the region (Lovett 1988). The area consists of montane, sub-montane evergreen, and deciduous primary and secondary forest, with the majority of the forest fragments < 25km<sup>2</sup> (Struhsaker *et al.* 2004; Ehardt *et al.* 2005). Annual rainfall averages 1,750 mm (Lovett 1996), of which 90% (1,650 mm) falls during the wet season from November to May (97 – 377 mm/wet season month; McCabe & Emery Thompson 2013). Food availability within the Udzungwa Mountains



**Figure 1.** An infant male Sanje mangabey consuming soil in the Udzungwa Mountains National Park. Photograph by Gráinne McCabe.

is influenced by rainfall with higher fruit availability occurring in the wet season (McCabe *et al.* 2013). A review by Msanya *et al.* (2002) identified ferric (containing iron), chromic (containing chromium), and eutric cambisols (soil horizon differentiation is weak, 39.7%) are the major constituents of the soil types of Tanzania; followed by rhodic (containing rhodium) and haplic ferralsols (red and yellow weathered soils, 13.4%) and humic (consisting of humus) and ferric acrisols (9.6%). This diverse assortment of soil types within a complex matrix is essential for the majority of proposed geophagy hypotheses.

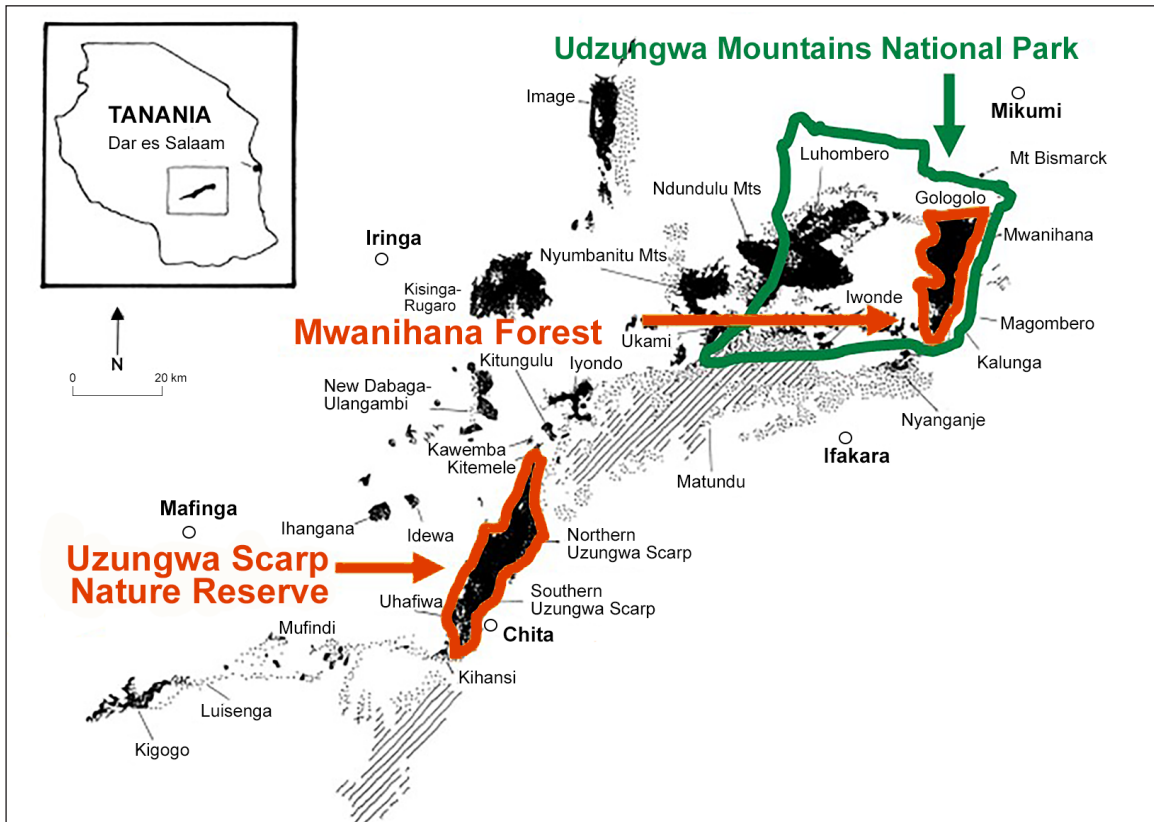
Sanje mangabeys are a medium-sized omnivore of the Papionini, endemic to the Udzungwa Mountains (Ehardt *et al.* 2005). The species is listed as endangered on the IUCN Red List of Threatened Species (McCabe *et al.* 2019). The diet of Sanje mangabeys within the Udzungwa Mountains National Park (UMNP) includes foods from 30 families, 52 genera, and 77 species of tree ( $n = 37$ ), climbers ( $n = 23$ ), shrubs ( $n = 14$ ), grasses ( $n = 2$ ), and fungi (species not quantified) (McCabe *et al.* 2013). Ripe fruit comprises 78% of consumed biomass, followed by seeds at 9%, then plant structural parts and flowers at 0.7% (McCabe *et al.* 2013). The remainder of the diet is fungi, invertebrates, and small vertebrates (McCabe 2012).

This research was conducted on a habituated group inhabiting the Mwanihana Forest ( $7^{\circ}40' - 7^{\circ}57'S$ ,  $36^{\circ}46' - 36^{\circ}56'E$ , Figure 2), where the largest sub-population of Sanje mangabey are found (Ehardt *et al.* 2005). Their home range (ca. 200 ha) lies within the boundaries of UMNP and elevation ranges from 300 – 2250 m a.s.l. (McCabe & Emery Thompson 2013). At the time of this study, the population consisted of approximately 63 to 65 individuals, including 7 to 10 adult males and 21 to 23 adult females. These mangabeys exhibit a polygamous mating system, and a social system where females are subordinate to males and female philopatry with male-biased dispersal is observed (Fernández *et al.* 2014). Mating and births occur throughout the year, however, 64% of conceptions occurred during January to March (McCabe *et al.* 2013).

#### **Food Availability, Average rainfall, and Elevation**

During the study period average monthly rainfall (mm) was recorded at Mizimu base camp using a Taylor® rain gauge. We recorded the elevation with the use of a handheld GPS (Garmin eTrex) recording all locations in which soil consumption was observed.

We used phenology data to characterise seasonal patterns of food availability. This was achieved through stratified random sampling of quadrats



**Figure 2.** Location of the study site in Udzungwa Mountains, Tanzania. Map modified from Marshall (2007).

within the study group's range (Chapman & Fedigan 1990). This method ensures less abundant habitat types are included at representative amounts in the sampled area. Each month, 12 ecological plots (25 x 25 m) were monitored for the production of ripe and unripe fruit, flowers, and young and mature leaves for all trees (>10 cm DBH), climbers (>1 m in length), and shrubs (>1 m in height), using a 5 point scale of crown cover (0 = no cover, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%; as per Whittaker method, Comiskey *et al.* 2000). Furthermore, 21 additional known mangabey food plant species (those underrepresented in the 12 phenology plots) were located and monitored monthly for phenology. In total, 688 mangabey food trees, shrubs, and climbers were monitored (see McCabe 2012 for a full list of monitored species).

To determine the size of food crops, the phenology score for each plant part, e.g., the score for ripe fruit, was multiplied by the diameter at breast height (DBH) in cm for each tree species monitored. This value was then multiplied by the density of each species within the plot per ha, to produce a Composite Phenology Score (CPS) (as per Wiczkowski & Kinnaird 2008). Fruit, both ripe and unripe, was the predominant component

of the mangabey diet (~80%); hence, we used fruit CPS as a proxy for monthly food availability. This then provided us with a quantitative score of food temporal availability, which can determine the relationship between seasonality and geophagy, as well the relationship between the abundance of PSMs and fibre in the diet, and geophagy.

### Statistical Analysis

A general linear model (GLM) was used to determine the relationship of fruit availability (ripe, unripe, and total fruit), elevation, and rainfall with the occurrence of deliberate soil consumption. The data used for GLM met all assumptions (normally distributed and independent of one another) required to perform the test (see Zuur *et al.* 2010). All statistical analyses were undertaken using R (R i386 version 3.3.3).

## RESULTS

### Seasonality and Pattern of Geophagy

During the study period rainfall ranged from 0 to 12.57 mm/month, with April showing the highest rate of precipitation. We found no relationship

**Table 1. Results of general linear model (GLM) on the effect of environmental characteristics (fruit availability, precipitation and elevation) on the occurrence of geophagic behaviours in the Sanje mangabey.**

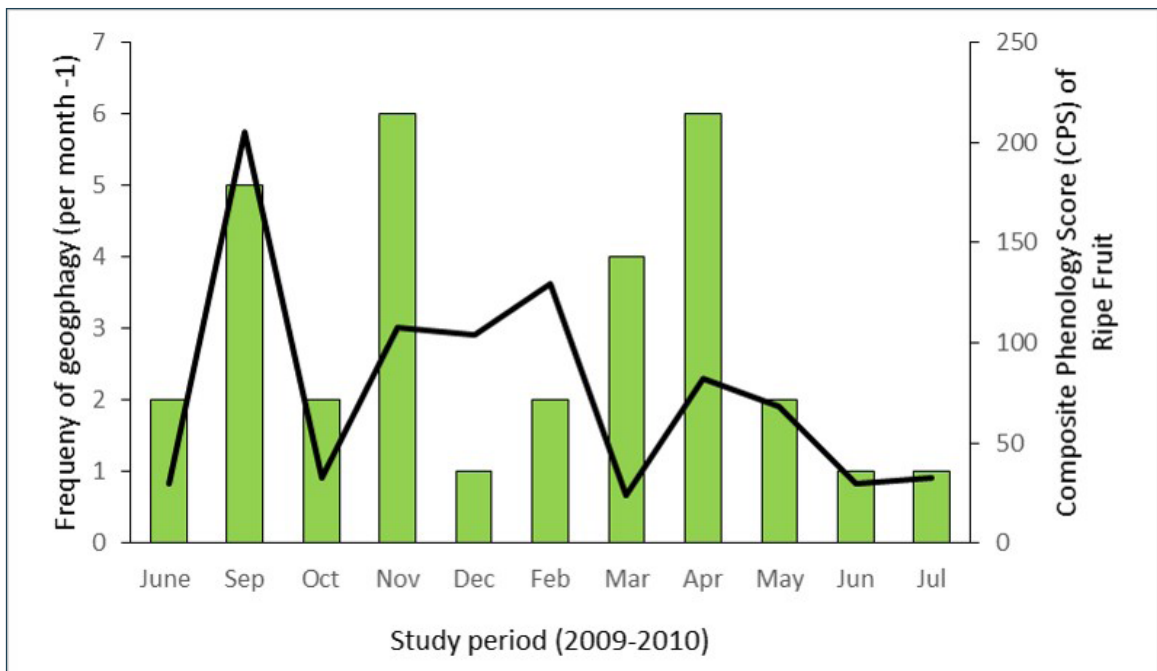
Fixed effects:	Estimate	SE	df	p-value
Intercept	2.246	0.569	-	-
Ripe fruit	-0.0017518	0.0007829	33	<b>0.032*</b>
Unripe fruit	0.0001581	0.0001280	33	0.225
Total fruit	0.00008388	0.0001382	33	0.548
Rainfall	0.0029520	0.0127522	29	0.818
Elevation	-0.0003963	0.0007809	29	0.615

\* Significant at  $p < 0.05$

between rainfall (mm) and the occurrence of geophagy; although, 70.58% of observed soil consumption ( $n = 21$ , November to May) occurred during the wet season. Similarly, the mangabeys did not show a preference for soil at particular elevations, as consumption was observed at sites ranging from 452 to 935 m, with average elevation of 768.8 m.

We found a significant positive relationship between available ripe-fruit and the occurrence of geophagy (GLM:  $F = -0.00175$ ,  $df = 33$ ,  $p = 0.032$ ), where the occurrence of observed soil

consumption decreased with the decrease in ripe fruit availability (Table 1). Furthermore, 70.58% of observed geophagy occurred between November to May, when fruit abundance was high (Figure 3). We observed an average Composite Phenology Score (CPS) of 192.32 for ripe fruit in the wet season and a relatively lower average score of 89.09 during the dry season (June to October). No significant relationship was observed between unripe fruit availability and occurrence of soil consumption.



**Figure 3.** Frequency of observed geophagy ( $n = 32$ ) in relation to available ripe fruit.

## DISCUSSION

Our results highlight several features and variations in soil consumption by the Sanje mangabeys that may provide insight into the role of geophagy in the Mwanihana Forest. Two potential hypotheses were introduced: those with a protective role and alleviation of GI distress. The patterns of soil consumption observed by the mangabeys may not be explained by one hypothesis alone, but rather a mixture of multiple explanations which are discussed below.

The Sanje mangabey is highly frugivorous with ripe fruit accounting for 71 to 85% of their diet annually (McCabe *et al.* 2013). This is contradictory to the protection hypothesis that states that soil consumption aids in the absorption of plant secondary metabolites (PSMs) and other plant toxins (Oates 1978; Wakibara *et al.* 2001). One of the main criteria of the “detoxification” hypothesis is that high levels of the diet contain toxic or anti-feedant properties. Typically, diets consisting of high amounts of fruit possess relatively low PSMs compared with diets of leaves and roots (Ehrlen & Eriksson 1993; Wink 1997). However, this will depend on fruit type and seed contents (Cipollini & Levey 1997). For example, Giliardi *et al.* (1999) found within parrots geophagy acted as a strategy to minimise intoxication from secondary plant compounds in seeds. Nevertheless, ripe fruits have evolved to maximise attractiveness to potential seed dispersers. Hence, high fruit PSMs would be deleterious to the plant’s reproductive success (Willey 2016).

Leaves are evolved to ensure optimum photosynthesis and production of ATP (adenosine triphosphate) and sugars (e.g., glucose), which is entirely or partially disrupted during defoliation from herbivores (Willey 2016). Subsequently, plants tend to accumulate PSMs within a leaf’s vacuoles, deterring defoliation, as secondary metabolites such as tannins inhibit protein within the mouth parts of many invertebrates (Arnason & Bernards 2010) and cause GI distress with vertebrates (Horowitz & Gentili 1969; Esaki *et al.* 1977; Vidal *et al.* 2004). Therefore, highly folivorous primates, such as leaf-eating monkeys that frequently encounter high concentrations of phenolics (e.g., flavonoids and tannins, Freeland & Janzen 1974) should disproportionately benefit from geophagy compared with highly frugivorous species. However, leaf-eating primates possess symbiotic bacteria within their foregut that can detoxify the PSMs and other

plant toxins that are associated with gastrointestinal upsets (Hladik 1977). The leaf-eating monkeys can further circumvent these problems, either by avoiding mature leaves high in plant toxins and preferentially targeting younger leaves (Oates 1977), or by consuming more seeds rather than leaves during the dry season where plant PSM concentrations are high (e.g., black colobus monkey, *Colobus satanus*, McKey 1978).

The majority of the Sanje mangabey’s high fruit diet is unlikely to consist of high concentrations of toxic plant compounds. However, it should be noted that McCabe *et al.* (2013) observed that fungi represented a relatively high percentage (11%) of the annual food intake. Fungi produce their own array of toxins and chemical deterrents which were not tested in this study. Hence, it is difficult to rule out the possible role of geophagy to combat the potential impact of fungal toxins.

Another criterion of the protection hypothesis is that ingested soils contain clay minerals, which can adsorb agents responsible for GI distress. High levels of clay minerals or porous soil are determined essential for the functionality proposed by the “detoxification” hypothesis (Wakibara *et al.* 2001). These geophagic materials act by decreasing GI distress, either through the direct absorption of toxic PSMs, parasites and pathogens, or actively preventing the transfer of harmful agents through luminal epithelium by coating the GI tract (Mahaney *et al.* 1993; Gilardi *et al.* 1999; Young *et al.* 2012). Furthermore, Ta *et al.* (2018) found the ability of clay to absorb PSMs depended on the polar potential of the compound or compound class, with compounds that possess a greater polarity being more readily absorbed. For example, highly polar compounds such as alkaloids and phenolics are easily absorbed. However, lipophilic terpenes by definition actively repel from water molecules, in turn reducing the possibility of clay absorption (a highly hydrophilic compound). They also observed that clays with a 2:1 (Si:Al) clay mineral (e.g., montmorillonite) were more effective at absorption, than the 1:1 of Kaolinite. Suggesting, the role of geophagic clays is reliant on the structure of interstitial spaces and polar potential of PSMs. Unfortunately, particle analysis was not undertaken with the Sanje mangabey samples due to logistical issues. However, qualitative descriptions for each sample were recorded with all “ingested” samples being described as containing no clay. Furthermore, the cryptic nature of geophagy (Pebsworth *et al.* 2012) makes the frequency of occurrence difficult to quantify. Subsequently, the

relatively low occurrence of the soil consumption in this study may not be representative of the extent of this behaviour within this population.

The deliberate consumption of soil has also been associated with relieving GI distress from reduced fibre diets, parasitic infection, and adjustments in pH (Wakibara *et al.* 2001). Diets high in soluble carbohydrates and proteins, but low in fibre, promote the buffering of gastric disorders, a decrease in pH, colonisation of advantageous GI microflora, and accelerated fermentation and associated increase in volatile fatty acids (Kreulen 1985). Studies on several species suggest that geophagy is highly seasonal and closely related to phenological changes in the habitat; occurring at greater frequencies in seasons of abundant young leaves and shoots (Kreulen 1985; Moe 1993). The low fibre content of the diet during these periods will increase the intake of soluble carbohydrates and proteins provoking gastric disorders, in turn, inducing geophagic behaviour (Hebert & Cowan 1971; Kreulen 1985). Ripe fruit tends to contain relatively low levels of fibre and high soluble carbohydrates, such as fructose (Willey 2016), and may stimulate the same reaction observed for young leaves.

The high ripe fruit contents within the mangabeys' diet suggest deliberate soil consumption may provide advantageous benefits to relieving GI discomfort. However, the majority of studies on the "alleviation of GI distress" hypothesis have focused on several kinds of clay minerals (Vermeer & Ferrell 1985; Johns 1986; Gilardi *et al.* 1999). They have suggested that clay-rich soils act by absorbing volatile fatty acids and buffering changes in pH, which in turn relieve GI distress associated with fibre-poor diets. However, non-clay soils may provide similar outcomes depending on their mineral contents. Soils rich in calcium have been shown to affect the pH within the stomach (Cancelliere *et al.* 2014) making it more alkaline, in turn increasing the pH level. Therefore, calcium may act as a buffer reagent maintaining a favourable pH with GI tract similar to the effects seen with clay-rich soils. The slight seasonal increase in soil consumption during high fruit availability requires more investigation of soil structure to fully rule out the "alleviating GI distress" hypothesis.

Our research did not take into consideration the intrinsic factors (e.g., sex, life-stage) that may be influencing this behaviour in the mangabeys. However, our anecdotal observations in the field have verified that infants, juveniles, sub-adults, and adults of both sexes perform geophagy. It should be

noted, however, that more detailed study is needed to determine if differences exist in the frequency of this behaviour and the amount consumed between age/sex classes.

## CONCLUSION

We were unable to provide evidence that suggests a "protection" function for geophagy in this species. Rather, our study suggests that the mangabeys' highly frugivorous diet, high in soluble carbohydrates and low in fibre, may cause GI distress, which soil consumption may alleviate, providing preliminary support for the "alleviating GI distress" hypothesis. This conclusion is supported by an increased rate (frequency of soil consumption per month) of geophagy during the period of high fruit availability. Further research, however, is needed to determine the impact of intrinsic factors on geophagy in this species, as well as (1) the soil adsorption ability of PSMs, (2) the identification of individual PSMs within the diet, and (3) micronutrients within ingested soils to fully understand the function of geophagy for the Sanje mangabey.

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